EFFECTS OF CONVECTIVE AND DISPERSIVE MIGRATION ON STABILITY OF INTERACTING SPECIES SYSTEM IN HETEROGENEOUS HABITATS

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OCTOBER, 1980

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A Thesis Submitted
in Partial Fulfilment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

By

SUNITA VERMA

to the

DEPARTMENT OF MATHEMATICS

INDIAN INSTITUTE OF TECHNOLOGY KANPUR

OCTOBER, 1980

CERTIFICATE

This is to certify that the matter embodied in the thesis entitled 'Effects of convective and dispersive migration on stability of interacting species system in heterogeneous habitats' by Miss Sunita Verma for the award of the Degree of Doctor of Philosophy of the Indian Institute of Technology, Kanpur, is a record of bonafide research work carried out by her under my supervision and guidance. The results embodied in this thesis have not been submitted to any other University or Institute for the award of any degree or diploma.

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ACKNOWLEDGEMENTS

I express my deep sense of gratitude to my thesis supervisor, Professor J.B. Shukla for his invaluable suggestions, constructive criticism and indefatigable guidance throughout the course of this thesis work.

I am thankful to Mr. G.L. Misra and Mr. S.K. Tewari for type cutting the stencils with great care and patience and Mr. A.N. Upadhyaya for neatly cyclostyling them.

October 1980. *SUNITA VERMA*

CONTENTS

CHAPTER I

GENERAL INTRODUCTION

1.1 INTRODUCTION

The evolution and existence of species has been the subject of scientific investigation since the days of Darwin. Earlier studies were mainly concerned with experimental observations and it is only in the beginning of twentieth centuary that attempts have been made to predict the evolution and existence of species mathematically. The first major attempt in this direction is due to Volterra and Lotka which constitute the main theme of the deterministic theory of population dynamics in theoretical Biology even today. Over the last fifty years, many complex models for two or more interacting species have been proposed on the basis of Lotka and Volterra models by taking into account the effects of crowding, age structure, time delay, functional response, switching etc. (Holling, 1965; Rescigno,1968; 1977; May,1971; Maynard Smith,1974; Gomatam, 1974; Freedman et al.,1976; Cushing,1976; Fred Brauer, 1977; Tansky, 1978; Juan, Lin et al. 1978 ; Goel et al., 1971).

It may be noted that Lotka-Volterra model focusses on population interactions at a point in space (habitat) ignoring movement (migration) which means a perfect mixing of the species in a given region. Mathematically, this is equivalent to

assuming that the dispersal rates are sufficiently high and the population in the habitat are well mixed. By assuming so, one ignores the essential aspects of species response to environmental and ecological changes it encounters in the habitat. Thus, Lotka Volterra type models discribe the situations which correspond to only laboratory conditions rather than real situations arising in natural environment. It may be noted here that even in the laboratory spatial variations may be essential for the coexistence of the species, (Huffaker, 1958, 1963).

In the following,therefore,an account of the literature related to migration of the species and its effects on their evolution and co-existence is presented.

1.2 EFFECTS OF MIGRATION

In nature, the real habitats could be both homogeneous and heterogeneous as regards to their environmental and ecological characteristics are concerned. Heterogeneity can arise due to topographical and geographical conditions. Seasonal climatic changes can also affect the heterogeneity of the habitat. In modern times due to rapid industrialization deforestation and other man made projects, our environment and ecology have been subjected to unrecoverable stresses destroying the natural habitats leading to extinction of certain rare species belonging to animal and plant kingdom. Due to these and related effects the tendency of the species living in the habitat therefore is

to migrate to better suited regions of the habitat for their survival and existence. In general the movement of the species in the habitat may arise due to factors such as crowding, over population, predator chasing prey, refuge and fugitive strategies. Migration may be caused due to cross wind in case of insects, stream of water in case of fishes, climatic conditions, flooding, draught, invasions, colonization etc. The initial distribution of the population densities or the favourable and unfavourable conditions around the habitat may also cause the migration of the species even in the homogeneous habitats.

The migration of the species in general can be studied by identifying it with convective and dispersive processes in both homogeneous and heterogeneous habitats. Since the habitats could be both heterogeneous and anistropic it may be remarked that the convective and dispersive abilities of the species may be different in different directions. Thus, a typical species may have convective and dispersive migration in a particular direction due to favourable environmental and ecological conditions in that direction but it may have no migration in other direction due to various hurdles inhibiting their movement.

The most general model for the evolution of interacting species which include interaction, age structure, time delay, convective and dispersive migration with space and time dependent characteristics could involve equations of various types, for

example differential (partial or ordinary), difference-differential, integro-differential equations, etc. which may include stochastic parameters also. These growth equations are already non-linear in nature due to interaction of the species and the migration terms can make them further nonlinear if density dependent dispersal is considered. To make these models compatible, certain type of boundary conditions are to be prescribed. These conditions depend upon the surroundings of the habitat i.e. whether it is surrounded by hostile environment or favourable environment.

The first successful attempt to study the migration of species mathematically is due to Skellam (1951) by identifying the migration of species by random dispersal. Since then several investigators studied the effects of migration on linear stability of interacting species system by considering Volterra type prey predator and competition models, (Kerner, 1959; Landahl, 1959; Segal and Jackson, 1972; Hadeler, 1974; Gopalsamy, 1977; Maynard Smith, 1974; Jacob Jorne, 1977-a).

In particular, Hadeler (1974) has studied the effects of dispersion on linear stability of interacting species in the one dimensional homogeneous finite habitat for prey predator model where the dispersion coefficients are equal and constant for the two species. It has been shown that effect of such dispersion is to stabilize the equilibrium state under non-homogeneous boundary conditions giving stable nonuniform spatial patterns. Also, the similar analysis has been carried out by

Gopalsamy (1977) for competing species in case of homogeneous finite and semi-infinite habitats. It is evident from his work that dispersive migration has no effect on the otherwise unstable equilibrium state in case of semi-infinite habitat while migration may stabilize the equilibrium state in the case of finite habitat. For unequal but constant dispersion coefficients of the two species, the linear stability analysis has also been carried out by Mimura and Nishida (1978), Jacob Jorne (1977-a) and it has been shown that possibility of dispersive instability may arise in such cases.

As pointed out earlier the habitats are not only heterogeneous but anisotropic also, the effects of variable dispersion in one and two dimensional habitats would have more implications on the stability and co-existence of species.

In nature there are sufficient evidences of density dependent dispersal of species as presented by Wolfenbarger et al. (1974), Krebs et al. (1974). Such effect on the stability of equilibrium state has been considered by various investigators, (Gurney and Nisbet, 1975, 1976; Gurtin and MacCamy, 1977) and it has been shown that it further stabilizes the equilibrium state.

The effects of ecological heterogeneity on prey predator system has also been investigated by Comins and Blatt (1974) by considering the habitat having both favourable and unfavourable regions leading to biased dispersion of the

species from unfavourable to more favourable regions, giving rise a term similar to convective migration in usual reaction diffusion equation. They have shown by numerical calculations that such biased dispersion of the species has an important stabilizing effect. Such biased dispersal can also arise if the species are migrating in a particular direction along a gradient of some environmental parameter such as wind in case of insects, Morris (1963), and water stream in case of fishes. The mathematical equation arising out of such biased dispersal has been derived by Mc Murtrie (1978).

Recently Mc Murtrie (1978) has given a detailed survey of literature regarding various aspects of dispersive and convective migration for one and two species system. The effects of dispersion in a heterogeneous habitat has also been surveyed by Levin (1974, 1976).

At this juncture it may be pointed out that the migration of a particular species in a habitat may also be affected by the dispersal of other species (cross dispersal), Kerner (1959). Rosen (1977-a) has studied such effect on interacting species systems with logarithmic dispersion term in the model.

Keeping this in view, in Chapter II, a generalized model has been proposed by considering density dependent self and cross-dispersion and its stability has been investigated both linearly and non-linearly (See summary, Chapter II, III and VII).

1.3 EFFECTS OF PATCHINESS

As pointed out earlier the real habitats are heterogeneo and could be inherently patchy due to discontinuous variations in topological, ecological and environmental characteristics. Since every continuum can be approximated by the finite sum of the sequence of constant functions even the habitat with continuously varying characteristics can be visualized as a patchy habitat with constant but different characteristics in different patches. It may, therefore, be very pertinent to ask, can the patchiness in the habitat confer stability to interacting species system with convective and dispersive migration terms?

In general, the behaviour of the interacting species as far as their interaction rates and migration rates are concerned could be different in different patches. In particular though it may happen that in one patch they have dispersive/convective ability while in other patch they may not have so due to certain unfavourable conditions in that patch. It can also be visualized that in the same patch convective migration may exist along one direction in the patch but not in other direction due to topographical, ecological and other conditions in the case of the two dimensional habitats. It can then happen, in some cases, as the patches are interconnected, that one patch may become the reservoir for the adjoining patch.

It can now be remarked that the equations governing the evolution of the species in each patch would be of the same form as in the case of single habitat but with different parameters in different patches. To find their solutions, suitable matching conditions have got to be prescribed at the various interfaces connecting the patches. These conditions normally are the continuity of population densities and fluxes at the interfaces. But due to certain topographical and other reasons the interfaces or barriers could be such that the densities may be continuous but not the fluxes.

Effects of patchiness in heterogeneous habitat on the stability, co-existence and other related aspects of interacting species have been studied by several investigators (Cohen, 1970; Levins and Culver, 1971; Horn and MacArthur, 1972; Vander Meer, 1973; Levin, 1974; 1976; Chewning, 1975; Maynard Smith, 1974; Kawasaki et al., 1979) by considering the movement of species from one patch to other as proportional to the difference of densities of the respective species in adjoining patches (passive dispersion). In particular, Levin (1974) has noted that over all species richness is expected to be higher in patchy environment. It has been pointed out by Kawasaki et al., (1979) that heterogeneity of environment and nonlinear diffusive motions play an important role in stabilizing the populations of competing species.

In the above mentioned studies the inherent dispersive ability of species in each of the patches which arises due to spatial variation causing density gradient within the patch has not been taken into account. Therefore, these studies may be useful only in cases where the patches are fairly narrow.

Keeping this in view, the effects of patchiness on linear and nonlinear stability of the equilibrium state of the system has been investigated in Chapters IV to VIII by considering various combinations of convection and dispersion in each of the patches with suitable matching at various interfaces [See summary].

1.4 LIAPUNOV STABILITY

In the previous two sections, we have described the literature regarding the effects of dispersal on the stability and co-existence of the species in homogeneous and heterogeneous (patchy) habitats which are mainly related to the study of linearized version of nonlinear models. To get the real insight of problems, the nonlinear system as a whole must be investigated. It is pointed out here that such coupled nonlinear systems cannot be solved analytically and one way to study their qualitative behaviour is by using Liapunov second method (LaSalle, 1961; Denn, 1975). This method has also been used even to study the linear stability of the equilibrium state of interacting systems (Gatto et al., 1977).

In population dynamics, to study the nonlinear stability of the equilibrium state Liapunov second method has been used by several investigators (Goh, 1976, 1977, Harrison 1979; Jacob Jorne et al.,1977, Hastings ,1978, Hsu, 1978,Gilpin ,1974).

In particular, the nonlinear stability of diffusive Lotka Volterra system has been carried out by Jacob Jorne et al. (1977), Gopalsamy et al. (1980) and it has been shown that the otherwise stable system remains stable with positive dispersion coefficients under zero flux boundary conditions.

Harrison (1979) has given a Liapunov function which generalizes the functions used by Volterra, Goh and Hsu and can be used to study the nonlinear stability of variety of models even with functional response. Kawasaki (1979) has used the Liapunov second method to study the nonlinear stability of the prey predator model in the case of patchy habitats with passive dispersion.

Keeping this in view in Chapters VII and VIII the linear and nonlinear stability of the interacting system in both homogeneous and heterogeneous habitats has been discussed by considering dispersive migration of the species with density and space dependence.

1.5 SUMMARY

In the present chapter, the survey of relevent literature has been presented so that the work done in this thesis can be seen in its proper prospective.

In Chapter II and III, the linear stability of interacting species with density dependent dispersal has been studied while in Chapter VII the corresponding Liapunov stability for linear and nonlinear systems has been investigated. The Chapters IV - VI are devoted to study the effects of space dependent dispersal of species on the linear stability by considering patchiness in habitats. The corresponding nonlinear analysis has been carried out in Chapter VIII.

In Chapter II, a generalized model for migrating species has been derived and it has been shown that in absence of cross-dispersion, an equilibrium state which is stable without dispersion is always stable with dispersion provided the dispersion coefficients of the two species are equal. However, when the dispersion coefficients of the two species are different, the possibility of self-dispersive instability arises. It has been also pointed out that the cross-dispersion of species may lead to stability or instability depending upon the nature and the magnitude of the cross-dispersive interactions in comparison to the self-dispersive interactions.

It has been shown that the self convective movement of species increases the stability of the equilibrium state and can stabilize an otherwise unstable equilibrium state. The effect of cross convection (in absence of self dispersion and self convection) is to stabilize the equilibrium state in a prey predator model with positive cross dispersion coefficients for the prey species.

Finally, it has been noted that if the system is stable under homogeneous boundary conditions it remains so under nonhomogeneous boundary conditions.

In Chapter III, the linear stability of two competing and migrating species in two dimensional finite and semi-infinite habitats is discussed under time dependent reservoir conditions and the conditions for stability of an equilibrium state with dispersion and convection derived.

In the case of prey-predator Volterra model an equilibrium state is shown to be stable with dispersion and convection in all cases.

In Chapter IV, the effect of space dependent dispersive migration on the linear stability of the equilibrium state of the system has been discussed by dividing the habitat into finitely many patches (subhabitats) where dispersion coefficient in each patch is assumed to be constant but different in different patches. This is reasonable because variable dispersion

coefficient can be approximated by the sum of finitely many unit step functions. It has been shown that the dispersion of competing species stabilizes an otherwise unstable equilibrium state in a patchy habitat under reservoir conditions along the boundary of the habitat. However, under flux boundary conditions the equilibrium state remains unstable. It has also been noted that the equilibrium state which is stable in two dimensional habitat may not be stable in a linear one dimensional habitat.

Chapter V deals with the effects of convection on the linear stability of competition and prey predator models in a two dimensional patchy habitat with transverse dispersion in all the patches. It has been shown for the competition model that with zero convective velocity of the species in a particular patch, the condition for stability is the same as in the case of one dimensional linear habitat. However, with nonzero convective velocity in a given patch, the equilibrium state may be stable or unstable depending upon the stability or instability in the preceeding patches. But if longitudinal convective velocity is zero in all the preceeding patches the equilibrium state is always stable.

In case of prey predator model, however, the equilibrium state is always stable in all the patches.

In Chapter VI, the linear stability of migrating species in a patchy habitat has been discussed by considering various

combinations of convection and dispersion in different patches.

In the case of one dimensional habitat with dispersion only in the last patch, it has been shown for competition model that an inherently unstable equilibrium state becomes stable in all patches in absence of dispersive migration. However, in the case of semi-infinite habitat the migration has no effect on the stability of the equilibrium state even in the presence of dispersion in the last patch. But when this patch is finite, a general condition for stability involving convective velocity and dispersion coefficient has been obtained.

In the case of two dimensional habitat consisting of only two patches, the linear stability of interacting system has been discussed with dispersion only in the last patch while transverse dispersion in both the patches. In the case of competition model, it has been shown that the stability of equilibrium state in the second patch is dependent on the conditions of its stability in the first patch and even if the equilibrium state is stable in the first patch, it may not be so in the second patch. But if the equilibrium state is unstable in the first patch, it would always be unstable in the second patch.

However, in the presence of equal longitudinal convection and dispersion of the species in all the patches, it has been shown that the effect of longitudinal convection is stabilizing in absence of transverse convection.

In Chapters VII, VIII, the linear and nonlinear stability of equilibrium state of interacting species system in a two dimensional finite habitat has been investigated for density and space dependent dispersal respectively by using Liapunov second method. It has been shown that conditions obtained for the linear stability are both necessary and sufficient. Further, the condition and region for nonlinear stability have also been derived in cases of competition and prey predator models.

Finally, it may be remarked here that the method developed and used in thesis can provide a new direction for studying non-linear partial differential equations with variable coefficients.

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CHAPTER II

EFFECTS OF CONVECTIVE AND DISPERSIVE INTERACTIONS ON THE LINEAR STABILITY OF TWO SPECIES SYSTEM

2.1 INTRODUCTION

As pointed out in Chapter I, the classical Volterra model for the evolution of two interacting species ignores the effects of migration which may arise due to environmental and ecological gradients in the habitat. These effects have been studied by taking into account the dispersive and convective migration terms in population models and the conditions for the linear stability of the equilibrium state derived for constant migration characteristics. (Skellam, 1951; Landahl, 1959; Segal and Jackson, 1972; Levin, 1974; Hadeler, 1974; Gopalsamy, 1977; Comins and Blatt, 1974). The importance of density dependent dispersal in the case of single species model has also been studied (Gurney and Nisbet, 1975) which may be selevent in anisotropic habitats.

It may be pointed out here that the evolution of a particular species not only depends upon the self dispersive migrations but is also affected by cross (biased or forced) dispersion which may arise due to dispersive migrations of other species (Kerner, 1959, Rosen, 1977,a,b) has studied

stability of the dynamic system by considering cross dispersion of the species, using Gomatam (1974) type interactions and generalized Fick's law involving logarithmic terms. Similar ideas have been exploited in chemical kinetics by Jacob Jorne (1974, 1975).

Keeping this in view, in this chapter, a generalized model for the interaction of two migrating species has been derived by considering self as well as cross dispersion effects. The linear stability of such a system is investigated by using Hurwitz criteria. Effects of convective migration of the species on the linear stability of systems have also been studied.

2.2 MATHEMATICAL MODEL

The equations governing the evolution of two interacting and dispersing species system in a heterogeneous habitat has been obtained by, Skellam (1951), as

$$\frac{\partial u_i}{\partial t} = f_i(u_1,u_2) - \nabla (\bar{J}_i); \quad i = 1,2 \qquad (2.1)$$

where u_1,u_2 denote the densities of the two species and the functions $f_i(u_1,u_2)$, $i = 1,2$ discribe the interactions of species. The flux vector $\bar{J}_i$ may be given by

$$\bar{J}_i = - \bar{D}_i \nabla u_i \qquad (2.2)$$

where $\bar{D}_i$ is the constant dispersion coefficient of the i^{th} species. Gurney and Nisbet (1975) have proposed that if the transport properties of species are nonlinear, the flux vector $\bar{J}_i$ may be generalized as

$$\bar{J}_i = -(\bar{D}_i + c_{ii}\, u_i)\nabla u_i \qquad i = 1,2 \qquad (2.3)$$

where c_{ii} is a constant. The second term may be interpreted as the dispersive interaction of the species with itself and may be termed as self dispersive interaction.

The evolution of species may also be affected by cross dispersive interactions (Kerner, 1959). To explain this point let us consider the prey predator model. Let u_1, u_2 denote the population of preys and predators respectively. In real situations the tendency of preys would be to keep away from the predators and as such the escape velocity of preys may be taken as proportional to the dispersive velocity of predators (Kerner, 1959). Also the tendency of predators would be to get closer to the preys and hence the chase velocity of predators may be assumed to be proportional to the dispersive velocity of preys. Keeping this in view, the following possibilities may arise.

(i) If the preys are escaping away with a velocity which is proportional to the dispersive velocity of the predators i.e. ∇u_2 and are having no encounters with the predators, their population is likely to increase. Therefore a term proportional to ∇u_2, (being negative) should be subtracted from the flux

vector $\bar{J}_1$ of preys [see equation (2.1) and (2.2)]. Similarly, if the predators are dispersing with the chase velocity which is proportional to the dispersive velocity of preys then, without encounters with preys, their population may decrease as they are wholy dependent on the prey population. In such a case, a term proportional to ∇u_1 (being negative) should be added in the population flux vector $\bar{J}_2$ of the predators.

(ii) While migrating with dispersive velocity proportional to ∇u_2, the predators may have a possibility of encounters with preys which is likely to increase the predator population. Due to this a term proportional to $u_1 \nabla u_2$ must be subtracted from $\bar{J}_2$, the flux vector of predators. Since this would happen at the cost of prey population, a similar term may be added to the prey population flux vector $\bar{J}_1$.

(iii) Similarly the preys while migrating with dispersive velocity proportional to ∇u_1 may have encounters with predators and therefore a term proportional to $u_2 \nabla u_1$ should be added to $\bar{J}_1$ as prey population is likely to decrease. Since this kind of interaction may increase the predators population, the similar term should be subtracted from the population flux vector $\bar{J}_2$ of predators.

Taking these points and the interaspecies dispersive interactions, given by (2.3), into account, the flux vector $\bar{J}_1$ and $\bar{J}_2$ for preys and predators respectively may be written as

$$\bar{J}_1 = -(\bar{D}_1+c_{11}u_1-c_{12}u_2)\ \nabla u_1-(\bar{d}_1-c_{21}u_1)\ \nabla u_2$$
$$\bar{J}_2 = -(\bar{D}_2+c_{22}u_2+e_{21}u_1)\ \nabla u_2+(\bar{d}_2-e_{12}u_2)\ \nabla u_1 \qquad (2.4)$$

where $\bar{D}_i$, $\bar{d}_i$, c_{ij}, e_{12}, e_{21}, $i,j=1,2$ are constant coefficients. Similar discussions are also applicable to other types of interactions such as competition.

Thus in general the flux vector of two interacting species can be written as follows:

$$\bar{J}_1 = -D_1(u_1,u_2)\ \nabla u_1 - d_1(u_1)\ \nabla u_2$$
$$\bar{J}_2 = -D_2(u_1,u_2)\ \nabla u_2 - d_2(u_2)\ \nabla u_1 \qquad (2.5)$$

It may be noted here that both the flux vectors may depend upon the density gradient of both the species and the self dispersion coefficients D_i and cross dispersion coefficients d_i, $i=1,2$ may be functions of population densities and can be positive and negative depending upon the types of dispersive interactions and their magnitudes [see equation (2.4)].

Now if the convective migration of both the species are also taken into account then it may be noted that due to this the fluxes $\bar{J}_i$ of the two species would increase by

$$\sum_{j=1}^{2} \vec{U}_{ij}\ u_j$$

where $\vec{U}_{ii}$ denotes the self convective velocity of ith species and $\vec{U}_{ij}\, i \neq j$ are convective velocities which might arise due

to environmental and ecological gradients and biased dispersions, (Comins and Blatt, 1974).

Thus, the flux equation (2.5) may be generalized as follows:

$$\begin{aligned} \bar{J}_1 &= -D_1(u_1,u_2)\ \nabla u_1 - d_1(u_1)\ \nabla u_2 + \bar{U}_{11}u_1 + \bar{U}_{12}u_2 \\ \bar{J}_2 &= -D_2(u_1,u_2)\ \nabla u_2 - d_2(u_2)\ \nabla u_1 + \bar{U}_{21}u_1 + \bar{U}_{22}u_2 \end{aligned} \qquad (2.6)$$

Thus, the equations governing the evolution of two species in a two dimensional habitat having environmental and ecological gradients can be written from (2.1) and (2.6) as

$$\frac{\partial u_1}{\partial t} + U_{1x}\frac{\partial u_1}{\partial x} + U_{1y}\frac{\partial u_1}{\partial y} + V_{1x}\frac{\partial u_2}{\partial x} + V_{1y}\frac{\partial u_2}{\partial y} = f_1(u_1,u_2) +$$

$$\frac{\partial}{\partial x}\left(D_{1x}\frac{\partial u_1}{\partial x}\right) + \frac{\partial}{\partial y}\left(D_{1y}\frac{\partial u_1}{\partial y}\right) + \frac{\partial}{\partial x}\left(d_{1x}\frac{\partial u_2}{\partial x}\right) + \frac{\partial}{\partial y}\left(d_{1y}\frac{\partial u_2}{\partial y}\right)$$

$$\frac{\partial u_2}{\partial t} + U_{2x}\frac{\partial u_2}{\partial x} + U_{2y}\frac{\partial u_2}{\partial y} + V_{2x}\frac{\partial u_1}{\partial x} + V_{2y}\frac{\partial u_1}{\partial y} = f_2(u_1,u_2) +$$

$$\frac{\partial}{\partial x}\left(D_{2x}\frac{\partial u_2}{\partial x}\right) + \frac{\partial}{\partial y}\left(D_{2y}\frac{\partial u_2}{\partial y}\right) + \frac{\partial}{\partial x}\left(d_{2x}\frac{\partial u_1}{\partial x}\right) + \frac{\partial}{\partial y}\left(d_{2y}\frac{\partial u_1}{\partial y}\right)$$

(2.7)

where D_{ix}, D_{iy} and d_{ix}, d_{iy}, $i=1,2$, are the self and cross dispersive coefficients and U_{ix}, U_{iy}, V_{ix}, V_{iy} denote the self and cross **convective** velocities in x and y directions respectively.

The spatially uniform equilibrium state $(\bar{u}_1, \bar{u}_2)$ of the system (2.7) is obtained by

$$f_1(\bar{u}_1,\bar{u}_2) = 0$$
$$f_1(\bar{u}_1,\bar{u}_2) = 0 \tag{2.8}$$

To study the local stability of the positive equilibrium state given by (2.8), the equation (2.7) may be linearized by using

$$u_i = \bar{u}_i + v_i \quad ; \; i = 1,2, \tag{2.9}$$

and neglecting the square and higher order terms to get,

$$\frac{\partial v_1}{\partial t} + U_{1x}\frac{\partial v_1}{\partial x} + U_{1y}\frac{\partial v_1}{\partial y} + V_{1x}\frac{\partial v_2}{\partial x} + V_{1y}\frac{\partial v_2}{\partial y} = \sum_{k=1}^{2} b_{1k}v_k$$
$$+ D_{1x}\frac{\partial^2 v_1}{\partial x^2} + D_{1y}\frac{\partial^2 v_1}{\partial y^2} + d_{1x}\frac{\partial^2 v_2}{\partial x^2} + d_{1y}\frac{\partial^2 v_2}{\partial y^2} \tag{2.10}$$
$$\frac{\partial v_2}{\partial t} + U_{2x}\frac{\partial v_2}{\partial x} + U_{2y}\frac{\partial v_2}{\partial y} + V_{2x}\frac{\partial v_1}{\partial x} + V_{2y}\frac{\partial v_1}{\partial y} = \sum_{k=1}^{2} b_{2k}v_k$$
$$+ D_{2x}\frac{\partial^2 v_2}{\partial x^2} + D_{2y}\frac{\partial^2 v_2}{\partial y^2} + d_{2x}\frac{\partial^2 v_1}{\partial x^2} + d_{2y}\frac{\partial^2 v_1}{\partial y^2}$$

where

$$b_{ik} = \left(\frac{\partial f_i}{\partial u_k}\right)_{\bar{u}_1,\bar{u}_2} , \; i,k = 1,2 \tag{2.11}$$

and v_i, $i=1,2$, are the small perturbations in population of the two species. Keeping in view the equation (2.4), it may be noted that the coefficients D_{ix}, D_{iy}, d_{ix}, d_{iy}, $i=1,2$ are functions of equilibrium values $\bar{u}_1$, $\bar{u}_2$, and may be positive or negative depending upon the type of interactions.

The linearized system (2.10) may be associated with the following initial conditions

$$v_i(x,y,0) = F_i(x,y) \quad ; \; i = 1,2 \tag{2.12}$$

For the finite habitat of dimensions $[0,L] \times [0,B]$, the nonhomogeneous reservoir conditions may be prescribed as

$$\left.\begin{aligned} v_i(x,y,t) &= N_{i1}(y) \quad \text{at} \quad x = 0 \\ v_i(x,y,t) &= N_{i2}(y) \quad \text{at} \quad x = L \end{aligned}\right\} \; 0 < y < B$$

$$\left.\begin{aligned} v_i(x,y,t) &= P_{i1}(x) \quad \text{at} \quad y = 0 \\ v_i(x,y,t) &= P_{i2}(x) \quad \text{at} \quad y = B \end{aligned}\right\} \; 0 < x < L \qquad t > 0 \tag{2.13-a}$$

or the flux conditions (when species are entering the habitat from outside) as

$$\left.\begin{aligned} -\frac{\partial v_i}{\partial x}(x,y,t) &= M_{i1}(y) \quad \text{at} \quad x = 0 \\ \frac{\partial v_i}{\partial x}(x,y,t) &= M_{i2}(y) \quad \text{at} \quad x = L \end{aligned}\right\} \; 0 < y < B$$

$$\left.\begin{aligned} -\frac{\partial v_i}{\partial y}(x,y,t) &= Q_{i1}(y) \quad \text{at} \quad y = 0 \\ \frac{\partial v_i}{\partial y}(x,y,t) &= Q_{i2}(y) \quad \text{at} \quad y = B \end{aligned}\right\} \; 0 < x < L \qquad t > 0 \tag{2.13-b}$$

In the following section, the local stability of the system (2.10) with above initial and homogeneous boundary conditions are discussed by ignoring the convective migration of the species. The self and cross dispersion coefficients are considered to be

constant with respect to the fixed equilibrium state $(\bar{u}_1, \bar{u}_2)$. The coefficients D_{ix}, D_{iy} are assumed to be positive while d_{ix}, d_{iy}, $i=1,2$ can be both positive or negative in all models in contrast to Rosen (1977 a,b).

2.3 EFFECTS OF DISPERSION ON STABILITY UNDER HOMOGENEOUS BOUNDARY CONDITIONS

To study the local stability of the system (2.10) without convection, let us write its solution, which satisfies the homogeneous reservoir conditions (2.13-a), i.e. $N_{ij} = P_{ij} = 0$; $i,j = 1,2$, as follows:

$$v_i(x,y) = \sum_{m=1}^{\infty} \sum_{n=1}^{\infty} e^{\lambda t} A_{imn} \sin \frac{m\pi x}{L} \sin \frac{n\pi y}{B}; \; i=1,2 \tag{2.14}$$

Substituting (2.14) in (2.10) (with convective velocities zero) we get the following characteristic polynomial for λ

$$\lambda^2 - \lambda\{b_{11}+b_{22}-(\sigma_1+\sigma_2)\} + b_{11}b_{22}-b_{12}b_{21}-b_{11}\sigma_2-b_{22}\sigma_1$$
$$+b_{21}\rho_1+b_{12}\rho_2+\sigma_1\sigma_2-\rho_1\rho_2 = 0 \tag{2.15}$$

$$\sigma_i = D_{ix}\frac{m^2\pi^2}{L^2} + D_{iy}\frac{n^2\pi^2}{B^2} \tag{2.16-a}$$

$$\rho_i = d_{ix}\frac{m^2\pi^2}{L^2} + d_{iy}\frac{n^2\pi^2}{B^2} \tag{2.16-b}$$

and $m,n = 1,2\ldots$.

Similarly, the solution of the system (2.10) (with convective velocities zero) under homogeneous flux boundary conditions

(2.13-b); i.e. $M_{ij} = 0 = Q_{ij}$, $i,j = 1,2$; can be written as

$$v_i = \sum_{m=0}^{\infty} \sum_{n=0}^{\infty} e^{\lambda t} B_{imn} \cos \frac{m\pi x}{L} \cos \frac{n\pi y}{B} \qquad (2.17)$$

which on substitution in equation (2.10) with $U_{ix} = U_{iy} = 0$, $V_{ix} = V_{iy} = 0$ give rise to the same characteristic polynomial as (2.15) with

$$\sigma_i = D_{ix} \frac{m^2\pi^2}{L^2} + D_{iy} \frac{n^2\pi^2}{B^2} \qquad (2.18\text{-a})$$

$$\rho_i = d_{ix} \frac{m^2\pi^2}{L^2} + d_{iy} \frac{n^2\pi^2}{B^2} \qquad (2.18\text{-b})$$

but $m,n=0,1,2,\ldots$

Using Hurwitz criteria, it may be noted from (2.15) that the equilibrium state given by (2.11) is stable, if the following conditions are satisfied,

$$b_{11} + b_{22} - (\sigma_1 + \sigma_2) < 0 \qquad (2.19\text{-a})$$

$$b_{11}b_{22}-b_{12}b_{21}-b_{11}\sigma_2-b_{22}\sigma_1+b_{21}\rho_1+b_{12}\rho_2+\sigma_1\sigma_2-\rho_1\rho_2 > 0 \qquad (2.19\text{-b})$$

For the case when there is no dispersion the above stability criteria simplify to

$$b_{11}+b_{22} < 0 \qquad (2.20\text{-a})$$

$$b_{11}b_{22}-b_{12}b_{21} > 0 \qquad (2.20\text{-b})$$

It is noted from (2.19) and (2.20) that an equilibrium state which is stable without dispersion would remain stable provided

(2.19-b) is satisfied, the possibility of which is real in the following cases.

(i) $\rho_1 \rho_2 < 0$ (2.21)

(ii) $D_{ix} \geq |d_{ix}|$, $D_{iy} \geq |d_{iy}|$, $i = 1,2$ (2.22)

In a particular case of (ii) i.e. for

$$\sigma_1 = \sigma_2 = \rho_1 = \rho_2 = \sigma \tag{2.23}$$

the otherwise stable state would remain so provided

$$b_{11}+b_{22} < b_{12}+b_{21} \tag{2.24}$$

The following cases are discussed in detail.

Case 1: Cross dispersion is absent.

In this case, $\rho_i = 0$; $i = 1,2$ and the conditions for stability of the equilibrium state simplify to

$$b_{11}+b_{22} - (\sigma_1 + \sigma_2) < 0 \tag{2.25-a}$$

$$b_{11}b_{22}-b_{12}b_{21}-b_{11}\sigma_2-b_{22}\sigma_1+\sigma_1\sigma_2 > 0 \tag{2.25-b}$$

Considering the case,

$$\left.\begin{aligned} D_{1x} &= D_{2x} = D_1 > 0 \\ D_{1y} &= D_{2y} = D_2 > 0 \end{aligned}\right\} \tag{2.26}$$

i.e. $\sigma_1 = \sigma_2 = \sigma > 0$

it can be noted that if conditions (2.20) are satisfied then conditions (2.25) are also valid. Hence, it is remarked that

equilibrium state which is stable without dispersion would always be stable with self dispersion provided the self dispersion coefficients are equal. But when the dispersion coefficients are different the condition (2.25-b) may not be satisfied even when the conditions (2.20) do indicating the possibility of dispersive instability. These results are valid both for reservoir and flux boundary conditions.

Considering the particular case, given by (2.26), under reservoir boundary conditions, the criteria for stability (2.25) become,

$$2\left(\frac{D_1}{L^2} + \frac{D_2}{B^2}\right) \pi^2 > b_{11} + b_{22} \qquad (2.27\text{-a})$$

$$2\left(\frac{D_1}{L^2} + \frac{D_2}{B^2}\right) \pi^4 > b_{11}^2 + b_{22}^2 + 2b_{12}b_{21} \qquad (2.27\text{-b})$$

after using the value of σ for the least values of m,n as unity. The condition (2.27-b) shows that the degree of the linear stability of the equilibrium state increases as the self dispersion coefficients increase, but it decreases as the size of habitat increases.

It is also noted that the conditions (2.25) can be satisfied irrespective of the conditions (2.20) and thus an unstable equilibrium state without dispersion may become stable with dispersion under reservoir conditions.

However if an equilibrium state without dispersion is unstable it would remain so under flux boundary conditions as

the stability conditions in this case are unaffected for at least $m=0$, $n=0$ [see equations (2.25) and (2.20)].

In a special case, when $b_{11}=0$, $b_{22}=0$, the corresponding characteristic polynomial (2.15) without dispersion $(\sigma_i=0)$ would have two complex conjugate roots with zero real parts for $b_{12}b_{21} < 0$ and the equilibrium state without dispersion is neutrally stable. In such a case, for $\sigma_i \neq 0$, $i = 1,2$ the conditions (2.25) are satisfied and the neutrally stable equilibriums state would become stable with dispersion. But if $b_{12}b_{21} > 0$ the roots of the corresponding characteristic equation (2.15) with $\sigma_i = 0$, $i=1,2$ would have one positive and one negative root and the equilibrium state is unstable. In such a case the condition (2.25) may be satisfied and an unstable state without dispersion would become stable with dispersion under reservoir conditions provided

$$\sigma_{11}\ \sigma_{21} - b_{12}b_{21} > 0$$

where σ_{11} and σ_{21} are the values of σ_1 and σ_2 for $m=n=1$.

Case II : Self dispersion is absent.

In this case $\sigma_i=0$, $i=1,2$ and the conditions for stability can be written as

$$b_{11} + b_{22} < 0 \tag{2.28-a}$$

$$b_{11}b_{22}-b_{12}b_{21}+b_{21}\rho_1+b_{12}\rho_2-\rho_1\rho_2 > 0 \tag{2.28-b}$$

where ρ_i can be both positive or negative. It is noted from

(2.20) and (2.28) that if an equilibrium state is stable without dispersion it would remain so with dispersion provided (2.28-b) is satisfied for all values of m,n. But it is possible to choose m,n such that (2.28-b) is never satisfied for the case when ρ_1 and ρ_2 are of the same sign and an equilibrium state which is stable without dispersion would not be stable with cross dispersion. However, if ρ_1 and ρ_2 are of opposite signs the condition (2.28-b) may be satisfied and the equilibrium state may become stable.

Further, if the system is unstable without cross dispersion, it may become stable under reservoir conditions provided (2.28-b) is satisfied and ρ_1, ρ_2 are of opposite signs. But with flux boundary conditions, an unstable equilibrium would never become stable.

2.4 PARTICULAR CASES

2.4.1 PREY-PERDATOR MODEL

To see the effects of dispersion in the case of prey predator model, the following form of functions $f_i(u_1,u_2)$, $i=1,2$ are prescribed.

$$\begin{aligned} f_1 &= (a_1 - b_1 u_1 - c_1 u_2)\, u_1 \\ f_2 &= (-a_2 - b_2 u_2 + c_2 u_1)\, u_2 \end{aligned} \tag{2.29}$$

where a_i, b_i, c_i are constants and u_1, u_2 denote the prey and

predator densities respectively. The spatially uniform equilibrium state of the system can be obtained from (2.8) as

$$\bar{u}_1, \bar{u}_2 = \frac{a_2c_1 + a_1b_2}{c_1c_2 + b_1b_2}, \quad \frac{a_1c_2 - a_2b_1}{c_1c_2 + b_1b_2} \tag{2.30}$$

for $a_1c_2 - a_2b_1 > 0$.

The constants b_{ij}; $i,j = 1,2$ in equation (2.10) can be found after using (2.11) as

$$\begin{aligned} b_{11} &= -b_1\bar{u}_1 \; ; \quad b_{12} = -c_1\bar{u}_1 \\ b_{21} &= \;\; c_2\bar{u}_2 \; ; \quad b_{22} = -b_2\bar{u}_2 \end{aligned} \tag{2.31}$$

It may be noted from (2.31), (2.20) and (2.25) that an otherwise stable equilibrium state is always stable with self dispersion and in absence of cross dispersion under both reservoir and flux boundary conditions.

Since d_{ix}, d_{iy}, $i=1,2$ can be both positive and negative the following possibilities arise.

$$\rho_1 > 0, \quad \rho_2 < 0 \tag{2.32-a}$$

$$\rho_1 < 0 \quad \rho_2 > 0 \tag{2.32-b}$$

$$\rho_1 > 0 \quad \rho_2 > 0 \tag{2.32-c}$$

$$\rho_1 < 0 \quad \rho_2 < 0 \tag{2.32-d}$$

Keeping in view (2.32-a) and using (2.31) it is noted that the conditions (2.20), (2.19) are always satisfied and the equilibrium state without dispersions would always be stable with self as

well as cross dispersions. These results are in line with the experimental work on prey-predator model by Huffaker (1958), Huffaker et al. (1963).

It may also be remarked here, by after noting equations (2.31), (2.19), (2.20) and (2.32-b,c,d), that the possibility of dispersive instability does exist.

2.4.2 COMPETITION MODEL

Considering the case of competition model, the interaction functions $f_i(u_1,u_2)$, $i=1,2$ are given by

$$\begin{aligned} f_1 &= (a_1-b_1u_1-c_1u_2)\,u_1 \\ f_2 &= (a_2-b_2u_2-c_2u_1)\,u_2 \end{aligned} \tag{2.33}$$

where a_i, b_i, c_i are positive interaction coefficients.

The positive nontrivial equilibrium point $(\bar{u}_1,\bar{u}_2)$ of the system (2.10) in this case is given by

$$\bar{u}_1,\bar{u}_2 = \frac{a_1b_2 - c_1a_2}{b_1b_2 - c_1c_2}\,,\quad \frac{a_2b_1 - c_2a_1}{b_1b_2 - c_1c_2} \tag{2.34}$$

for $$\frac{b_1}{c_2} > \frac{a_1}{a_2} > \frac{c_1}{b_2} \tag{2.35-a}$$

or $$\frac{b_1}{c_2} < \frac{a_1}{a_2} < \frac{c_1}{b_2} \tag{2.35-b}$$

The constants defined in equation (2.10) for this model after using the functions in (2.33) can be obtained from (2.11) as

$$b_{11} = -b_1\bar{u}_1 \quad ; \quad b_{12} = -c_1\bar{u}_1$$
$$b_{21} = -c_2\bar{u}_2 \quad ; \quad b_{22} = -b_2\bar{u}_2 \qquad (2.36)$$

Keeping in view (2.36) and (2.35-a), it is noted from the condition (2.20) that the equilibrium state (2.34) in absence of dispersion is stable. The stability of this system is further enhanced in presence of self dispersion and without cross dispersion [see equation (2.25)]. However under the condition (2.35-b) the equilibrium state (2.34) is not stable as the condition (2.20-b) is violated. In such a case the equilibrium state may become stable with self dispersion provided the condition (2.25-b) is satisfied.

Considering also the effects of cross dispersion and noting the signs of d_{1x}, d_{2x}, d_{1y}, d_{2y} for this model, it is seen that either ρ_1 and ρ_2 are of opposite signs (one competitor is superior than the other and having gains due to cross dispersive mobility) or both are negative. Then, in the former case the stable equilibrium state in the case of nonzero intraspecies interactions and without dispersion may remain stable provided (2.19-b) is satisfied. But in the later case it would become unstable as (2.19-b) is never satisfied for all values of m and n. However, if the equilibrium state is unstable without dispersion it may become stable with dispersion provided (2.19-b) satisfied in the case of reservoir conditions. But the unstable equilibrium state remains unstable for ρ_1, ρ_2 with same signs under flux boundary conditions.

2.5 EFFECTS OF CONVECTION ON STABILITY UNDER HOMOGENEOUS BOUNDARY CONDITIONS

In real situations the two interacting species may have different convective and dispersive abilities and it may be reasonable to postulate that the species having more convective velocity can disperse faster. It can then happen that the ratios of convective and dispersive velocities of the two species may be equal.

To visualize the difference between the effects of this relevent case and the case of equal migration characteristics, on the linear stability of the equilibrium state, the following cases are studied.

i. Equal convective velocities and dispersion coefficients of the two species.

ii. Unequal convective velocities and dispersion coefficients with their ratios being equal.

To avoid complexities the cases of self and cross migrations are dealt with separately.

2.5.1 EFFECTS OF SELF CONVECTION AND DISPERSION

To see the effects of convection on the stability of the equilibrium state, system (2.10) in absence of cross dispersion and cross convection can be written as follows

$$\frac{\partial v_1}{\partial t} + U_{1x}\frac{\partial v_1}{\partial x} + U_{1y}\frac{\partial v_1}{\partial y} = \sum_{k=1}^{2} b_{1k}v_k + D_{1x}\frac{\partial^2 v_1}{\partial x^2} + D_{1y}\frac{\partial^2 v_1}{\partial y^2}$$

$$\frac{\partial v_2}{\partial t} + U_{2x}\frac{\partial v_2}{\partial x} + U_{2y}\frac{\partial v_2}{\partial y} = \sum_{k=1}^{2} b_{2k}v_k + D_{2x}\frac{\partial^2 v_2}{\partial x^2} + D_{2y}\frac{\partial^2 v_2}{\partial y^2} \qquad (2.37)$$

where b_{ik}; $k=1,2$ is defined as in (2.11).

Considering the case,

$$U_{1x} = U_{2x} = U_1 \ , \ U_{1y} = U_{2y} = U_2 \ ,$$

$$D_{1x} = D_{2x} = D_1 \ , \ D_{1y} = D_{2y} = D_2 \ , \qquad (2.38)$$

the solution of the system (2.37) with (2.38) satisfying the homogeneous reservoir conditions (2.13-a) (i.e. $N_{ij} = P_{ij} = 0$; $i,j = 1,2$) can be written as

$$v_i = \sum_{m=1}^{\infty}\sum_{n=1}^{\infty} \bar{A}_{imn} \exp\left[\frac{U_1}{2D_1}x + \frac{U_2}{2D_2}y - \lambda t\right] \sin\left(\frac{m\pi x}{L}\right) \sin\left(\frac{n\pi y}{B}\right)$$

$$i = 1,2 \qquad (2.39)$$

Substitution of (2.39) in the system (2.37) give rise to the following characteristic polynomial in λ

$$\lambda^2 - \lambda\{\bar{b}_{11}+\bar{b}_{22}-2\sigma\} + \bar{b}_{11}\bar{b}_{22} - b_{12}b_{21} - (\bar{b}_{11}+\bar{b}_{22})\sigma + \sigma^2 = 0 \qquad (2.40)$$

where

$$\bar{b}_{11} = b_{11} - \left(\frac{U_1^2}{4D_1} + \frac{U_2^2}{4D_2}\right)$$

$$\bar{b}_{22} = b_{22} - \left(\frac{U_1^2}{4D_1} + \frac{U_2^2}{4D_2}\right) \qquad (2.41)$$

which gives the conditions for stability of the equilibrium as follows:

$$\bar{b}_{11}+\bar{b}_{22}-2\sigma < 0$$
$$\bar{b}_{11}\bar{b}_{22}-b_{12}b_{21}-(\bar{b}_{11}+\bar{b}_{22})\,\sigma + \sigma^2 > 0 \tag{2.42}$$

It can be seen that for $U_1=U_2=0$ this condition is equivalent to the conditions (2.25) with $\sigma_1=\sigma_2=\sigma$. It can therefore be noted from (2.42) that if the system is stable without convection it will remain stable with convection also and the degree of stability increases as the magnitude of convective velocity increases. It is further noted from (2.42) that if the system is unstable without convection it may become stable with convection provided (2.42) is satisfied.

Considering the second case, when the convection and dispersion of the two species are not equal but the ratios of dispersion coefficient to the convective velocity for the two species are equal i.e.

$$\frac{U_{1x}}{D_{1x}} = \frac{U_{2x}}{D_{2x}}\,,\quad \frac{U_{1y}}{D_{1y}} = \frac{U_{2y}}{D_{2y}} \tag{2.43}$$

the solution of the system (2.37) satisfying homogeneous reservoir conditions (2.13-a) can be written as

$$v_i(x,y,t) = \sum_{m=1}^{\infty}\sum_{n=1}^{\infty} A^*_{imn} \exp\left[\frac{U_{ix}}{2D_{ix}}\,x + \frac{U_{iy}}{2D_{iy}}\,y + \lambda t\right]$$
$$\sin\left(\frac{m\pi x}{L}\right)\sin\left(\frac{n\pi y}{B}\right)$$
$$i = 1,2. \tag{2.44}$$

which on substitutiong in the system (2.37) give rise to the following characteristic polynomial in

$$\lambda^2 - \lambda\{b_{11}^* + b_{22}^* - (\sigma_1 + \sigma_2)\} + b_{11}^* b_{22}^* - b_{12} b_{21} - (b_{11}^* \sigma_2 + b_{22}^* \sigma_1) + \sigma_1 \sigma_2 = 0 \tag{2.45}$$

where

$$b_{ii}^* = b_{ii} - \frac{U_{ix}^2}{4D_{ix}} - \frac{U_{iy}^2}{4D_{iy}} \tag{2.46}$$

The conditions for stability in this case can be derived as follows:

$$\begin{aligned} & b_{11}^* + b_{22}^* - (\sigma_1 + \sigma_2) < 0 \\ & b_{11}^* b_{22}^* - b_{12} b_{21} - (b_{11}^* \sigma_2 + b_{22}^* \sigma_1) + \sigma_1 \sigma_2 > 0 \end{aligned} \tag{2.47}$$

Since the condition (2.47) is of similar form as that of (2.42), it can be remarked here that unequal convection also stabilizes the equilibrium state. Thus, it may be remarked that the difference between the two above mentioned cases are only quantitative in nature and qualitatively convection (in both the cases of equal and unequal convection) has stabilizing effect.

2.5.2 EFFECTS OF CROSS CONVECTION AND DISPERSION

Let us write the system (2.10) in absence of self convection and self dispersion as

$$\frac{\partial v_1}{\partial t} + V_{1x}\frac{\partial v_2}{\partial x} + V_{1y}\frac{\partial v_2}{\partial y} = \sum_{k=1}^{2} b_{1k}v_k + d_{1x}\frac{\partial^2 v_2}{\partial x^2} + d_{1y}\frac{\partial^2 v_2}{\partial y^2}$$

$$\frac{\partial v_2}{\partial t} + V_{2x}\frac{\partial v_1}{\partial x} + V_{2y}\frac{\partial v_1}{\partial y} = \sum_{k=1}^{2} b_{2k}v_k + d_{2x}\frac{\partial^2 v_1}{\partial x^2} + d_{2y}\frac{\partial^2 v_1}{\partial y^2} \qquad (2.48)$$

Considering a particular case of (45),

$$d_{1x} = d_{2x} = d_1 \qquad d_{1y} = + d_{2y} = d_2$$

$$V_{1x} = V_{2x} = V_1 \qquad V_{1y} = + V_{2y} = V_2 \qquad (2.49)$$

the solution of the system (2.48) with (2.49) under reservoir conditions can be written as

$$v_i = \sum_{m=1}^{\infty}\sum_{n=1}^{\infty} \bar{B}_{imn}\exp\left(\frac{V_1}{2d_1}x + \frac{V_2}{2d_2}y + \lambda t\right)\sin\left(\frac{m\pi x}{L}\right)\sin\left(\frac{n\pi y}{B}\right) \qquad (2.50)$$

Substitution of (2.50) in (2.48) with (2.49) give rise to the following characteristic polynomial in λ

$$\lambda^2 - \lambda(b_{11}+b_{22}) + b_{11}b_{22} - \bar{b}_{12}\bar{b}_{21} + \rho(\bar{b}_{12}+\bar{b}_{21}) + \rho^2 = 0 \qquad (2.51)$$

where

$$\bar{b}_{12} = b_{12} - \frac{V_1^2}{4d_1} - \frac{V_2^2}{4d_2}$$

$$\bar{b}_{21} = b_{21} - \frac{V_1^2}{4d_1} - \frac{V_2^2}{4d_2} \qquad (2.52)$$

Thus the criteria for stability of the equilibrium state in this case can be written as

$$b_{11}+b_{22} < 0$$
$$b_{11}b_{22}-\bar{b}_{12}\bar{b}_{21}+\rho(\bar{b}_{12}+\bar{b}_{21})-\rho^2 > 0 \qquad (2.53)$$

It can be noted from (2.53) that the equilibrium state which is unstable without cross convection remains so with cross convection also.

Considering the next interesting case when the convection and dispersion of the two species are not equal but the following relations between cross dispersion and convection hold

$$\frac{V_{1x}}{d_{1x}} = \frac{V_{2x}}{d_{2x}} \; ; \quad \frac{V_{1y}}{d_{1y}} = \frac{V_{2y}}{d_{2y}} \qquad (2.54)$$

Then, the solution of the system (2.48) under resevoir conditions can be assumed as

$$v_i(x,y,t) = \sum_{m=1}^{\infty}\sum_{n=1}^{\infty} B^*_{imn} \exp\left[\frac{V_{ix}}{2d_{ix}}x + \frac{V_{iy}}{2d_{iy}}y + \lambda t\right] \sin\left(\frac{m\pi x}{L}\right)\sin\left(\frac{n\pi y}{B}\right) \qquad (2.56)$$

which on substitution in (2.45) gives the following characteristic equation for λ

$$\lambda^2-\lambda(b_{11}+b_{22})+b_{11}b_{22}-b^*_{12}b^*_{21}+(\rho_2 b^*_{12}+\rho_1 b^*_{21})-\rho_1\rho_2 = 0 \qquad (2.57)$$

where

$$b_{12}^{*} = b_{12} - \frac{V_{1x}^{2}}{4d_{1x}} - \frac{V_{1y}^{2}}{4d_{1y}}$$
$$b_{21}^{*} = b_{21} - \frac{V_{2x}^{2}}{4d_{2x}} - \frac{V_{2y}^{2}}{4d_{2y}} \qquad (2.58)$$

and the conditions for stability in this case are obtained as

$$b_{11}+b_{22} < 0$$
$$b_{11}b_{22}-b_{12}^{*}b_{21}^{*} + (\rho_2 b_{12}^{*} + \rho_1 b_{21}^{*}) - \rho_1\rho_2 > 0 \qquad (2.59)$$

Keeping in view of (2.53), it can be noted from (2.59) that when the cross dispersion coefficients are of opposite signs as in the case of preypredator model (Kerner, 1959), the equilibrium state which is unstable with equal cross convection and dispersion may become stable with unequal cross convection and dispersion.

2.6 EFFECTS OF NONHOMOGENEOUS BOUNDARY CONDITIONS

To see the effects of nonhomogeneous boundary conditions (2.13) on the local stability of the system (2.10), we prove the following theorem.

Theorem : If the linearized system (2.10) with homogeneous boundary conditions is stable it would remain so even under time independent nonhomogeneous boundary conditions (2.13).

Proof : Let $v_i(x,y,t)$, $i = 1,2$ be the solution of the system (2.10) with the initial condition (2.12) and the boundary

conditions (2.13-a) or (2.13-b). Let $\bar{v}_i(x,y)$ be the steady state solution of the corresponding system (2.10) satisfying nonhomogeneous boundary conditions (2.13-a) or (2.13-b). Then, it can be noted from (2.10) and its corresponding steady state that

$$z_i(x,y,t) = v_i(x,y,t) - \bar{v}_i(x,y), \; i = 1,2 \tag{2.60}$$

would also satisfy the system (2.10) with the following initial conditions,

$$z_i(x,y,0) = v_i(x,y,0) - \bar{v}_i(x,y), \; i = 1,2. \tag{2.61}$$

and the homogeneous boundary conditions corresponding to (2.13).

Since the forms of $z_i(x,y,t)$, $i = 1,2$ would be the same as that of $v_i(x,y,t)$, it is noted from equation (2.60) that the conditions for stability under both homogeneous and time independent non-homogeneous boundary conditions would remain the same.

2.7 CONCLUSIONS

The evolution and local stability of two interacting species in a heterogeneous environment have been investigated by taking into account the effects of self as well as cross dispersions and convections under reservoir and flux conditions prescribed at the boundary of the finite two dimensional habitat.

Effects of dispersion (in absence of convection) on the stability of the equilibrium state have been summarised in Table 1.

Effects of self convection (in absence of cross dispersion and convection) have also been investigated and it has been shown that it generally stabilizes the system under both type of boundary conditions. In particular, it has been noted that a stable equilibrium state without self convection becomes more stable while an unstable equilibrium state may become stable with convection.

Effect of cross convection (in the absence of self dispersion and self convection) on the prey-predator model is to stabilize the equilibrium state.

Further, it is noted that for equal dispersion coefficients and convective velocities the equilibrium state remains unstable [see equation (2.53)].

A particular case of unequal convection and dispersion, when the ratios of dispersion coefficients to the convective velocities for the two species are equal, has been discussed and it has been shown that the equilibrium state which is unstable with equal self and cross dispersion may become stable in this case.

It has also been shown that if the system is stable with homogeneous boundary conditions it remains so under time independent non-homogeneous boundary conditions.

Table 1 : Effects of dispersion in absence of convection

Cases	Nature of coefficients of self-dispersion	Nature of coefficients of cross dispersion	Remark about the stability of the equilibrium state without dispersion	Remark about the stability of the equilibrium state with dispersion	
				Reservoir conditions	Flux conditions
1	$D_{ix}>0; D_{1x}\neq D_{2x}$ $D_{iy}>0, D_{1y}\neq D_{2y}$	$d_{ix}=0, i=1,2$ $d_{iy}=0$	I stable II unstable	stable under (2.25b) stable under (2.25)	stable with (2.25-b) unstable
2	$D_{1x}=D_{2x}=D_1>0$ $D_{1y}=D_{2y}=D_2>0$	$d_{ix}=0, i=1,2$ $d_{iy}=0$	I stable II unstable	stable stable under (2.27)	stable unstable
3	$D_{ix}=0; i=1,2$ $D_{iy}=0$	$d_{1x}>0; d_{2x}>0$ $d_{1y}>0; d_{2y}>0$	I stable II unstable	unstable unstable	unstable unstable
4	$D_{ix}=0, i=1,2$ $D_{iy}=0$	$d_{1x}>0; d_{2x}<0$ $d_{1y}>0; d_{2x}<0$ or $d_{1x}<0; d_{2x}>0$ $d_{1y}<0; d_{2x}<0$	I stable II unstable	stable under (2.28-b) stable under (2.28)	stable under (2.28-b) unstable
5	$D_{ix}>0; i=1,2$ $D_{iy}>0$	$d_{ix}, d_{iy}; i=1,2$ satisfying (2.21) or (2.22)	I stable II unstable	stable under (2.19-b) stable under (2.19)	stable under (2.19-b) unstable

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CHAPTER III

STABILITY OF TWO INTERACTING AND MIGRATING SPECIES SYSTEM IN TWO DIMENSIONAL HABITATS

3.1 INTRODUCTION

In the previous chapter, the effects of self and cross dispersion and convection on the linear stability of two interacting species system have been discussed in a two dimensional finite habitat and the criteria for stability of the equilibrium state derived under homogeneous and non-homogeneous constant boundary conditions. It can be noted, however, that neither the density distributions of the species in the habitat have been found nor the effects of time dependent boundary conditions have been investigated.

In this chapter, therefore, the linear stability of two interacting and migrating species system without cross convection and dispersion is carried out in finite and semi-infinite habitats under time dependent nonhomogeneous boundary conditions. The steady and unsteady state distributions of the species are obtained. A special case when the dispersion coefficient in a particular direction is zero has also been investigated.

3.2 BASIC EQUATIONS

The system governing the evolution of two interacting and migrating species in a two dimensional anisotropic habitat $(0 < x < L,\ y > 0)$ can be written as

$$\frac{\partial u_i}{\partial t} + U_i \frac{\partial u_i}{\partial x} + V_i \frac{\partial u_i}{\partial t} = f_i(u_1,u_2) + \frac{\partial}{\partial x}\left[D_{ix}(u_1,u_2)\frac{\partial u_i}{\partial x}\right] + \frac{\partial}{\partial y}\left[D_{iy}(u_1,u_2)\frac{\partial u_i}{\partial y}\right] \quad (3.1)$$

where u_i, $i = 1,2$ denotes the density of ith species at any point (x,y) in the habitat at an instant t; U_i , V_i , the convective velocity components and D_{ix}, D_{iy} , the dispersal coefficients in x (longitudinal) and y (transverse) directions respectively which may be, in general, functions of u_1,u_2. The function $f_i(u_1,u_2)$; $i = 1,2$ denotes the interaction term for ith species.

The nontrivial positive equilibrium point of the system (3.1) is given by

$$f_i(\bar{u}_1,\bar{u}_2) = 0;\ i = 1,2 \quad (3.2)$$

Keeping in view of (3.2) and writing,

$$u_i(x,y,t) = \bar{u}_i + v_i\ (x,y,t) \quad (3.3)$$

the system (3.1) can be linearized about the equilibrium state as follows :

$$\frac{\partial v_i}{\partial t} + U_i \frac{\partial v_i}{\partial x} + V_i \frac{\partial v_i}{\partial y} = \sum_{k=1}^{2} b_{ik} v_k + D_{ix}(\bar{u}_1,\bar{u}_2) \frac{\partial^2 v_i}{\partial x^2} + D_{iy}(\bar{u}_1,\bar{u}_2) \frac{\partial^2 v_i}{\partial y^2} \qquad (3.4)$$

where

$$b_{ij} = \left.\frac{\partial f_i}{\partial u_j}\right|_{\bar{u}_1,\bar{u}_2} ; \; i, j = 1,2 .$$

It is noted here that the dispersion coefficients in (3.4) are functions of $(\bar{u}_1,\bar{u}_2)$ and are constant for fixed equilibrium state.

The following initial and boundary conditions for the system (3.4) can be prescribed,

$$v_i(x,y,0) = 0; \; i = 1,2 \; ; \; 0 < x < L, \; 0 < y < B \qquad (3.5)$$

$$v_i(0,y,t) = 0; \; i = 1,2 \; ; \; 0 < y < B, \; t > 0 \qquad (3.6)$$

$$v_i(L,y,t) = 0; \; i = 1,2 \; ; \; 0 < y < B, \; t > 0 \qquad (3.7)$$

$$\left.\begin{aligned} v_1(x,0,t) &= N(t) \\ v_2(x,0,t) &= P(t) \end{aligned}\right\} \; 0 < x < L; \; t > 0 \qquad (3.8)$$

such that

$$\underset{t \to \infty}{\mathrm{Lt}} N(t) = N_o, \quad \underset{t \to \infty}{\mathrm{Lt}} P(t) = P_o \qquad (3.9)$$

$$v_i(x,B,t) = 0; \; i = 1,2; \; 0 < x < L; \; t > 0 \qquad (3.10\text{-a})$$

for finite habitat

or

$$\underset{y \to \infty}{\mathrm{Lt}} v_i(x,y,t) = 0; \; i = 1,2 \; ; \; 0 < x < L; \; t > 0 \qquad (3.10\text{-b})$$

for the semi infinite habitat in y direction.

As in the previous chapter, the linear stability of the system (3.4) is investigated for the competition and prey predator models in the following two cases :

1. When the dispersion coefficients and convective velocities of the two species are equal.
2. When the ratios of dispersion coefficients to the convective velocities for the two species are equal.

3.3 COMPETITION MODEL

In the case of competing species the interaction functions f_1, f_2 may be prescribed as

$$\begin{aligned} f_1 &= u_1 \, (a_1 - c_1 u_2) \\ f_2 &= u_2 \, (a_2 - c_2 u_1) \end{aligned} \qquad (3.11)$$

and the linearized system for the evolution of two species would be given by (3.4) with

$$\begin{aligned} b_{ii} &= 0 \; ; \; i = 1,2 \\ b_{12} &= -f = -c_1 a_2 / c_2 < 0 \\ b_{21} &= -g = -c_2 a_1 / c_1 < 0 \end{aligned} \qquad (3.12)$$

3.3.1 EQUAL CONVECTION AND DISPERSION

Considering the case

$$
\begin{aligned}
D_{ix} &= D_1 \\
D_{iy} &= D_2 \\
U_i &= U \qquad ; \quad i = 1,2 \\
V_i &= V
\end{aligned}
\tag{3.13}
$$

and using the nonsingular matrix transformation $D_1 \neq 0$, $D_2 \neq 0$ for $U_1 \neq 0$, $U_2 \neq 0$)

$$
\begin{aligned}
X &= \exp\left[\frac{U}{2D_1}x + \frac{V}{2D_2}y - \left(\frac{U^2}{4D_1} + \frac{V^2}{4D_2}\right)t\right] AX_1 \\
X_1 &= \exp\left[\left(\frac{U^2}{4D_1} + \frac{V^2}{4D_2}\right)t - \left(\frac{U}{2D_1}x + \frac{V}{2D_2}\right)y\right] A^{-1} X
\end{aligned}
\tag{3.14}
$$

where,

$$
X = \begin{bmatrix} v_1(x,y,t) \\ v_2(x,y,t) \end{bmatrix} \quad ; \quad X_1 = \begin{bmatrix} w_1(x,y,t) \\ w_2(x,y,t) \end{bmatrix}
$$

$$
A = \begin{bmatrix} r\cosh(st) & \sinh(st) \\ -\sinh(st) & -1/r\cosh(st) \end{bmatrix}
$$

$$
r = \sqrt{f/g} \quad ; \quad s = \sqrt{fg}
$$

the system (3.4) with (3.12) reduces to the following form,

$$\frac{\partial w_i}{\partial t} = D_1 \frac{\partial^2 w_i}{\partial x^2} + D_2 \frac{\partial^2 w_i}{\partial y^2} \; ; \; i = 1,2 \tag{3.15}$$

The initial and boundary conditions (3.5) - (3.10) are transformed as follows :

$$w_i(x,y,0) = 0 \tag{3.16}$$

$$w_i(0,y,t) = 0 \tag{3.17}$$

$$w_i(L,y,t) = 0 \tag{3.18}$$

$$w_1(x,0,t) = \exp\left[-\frac{Ux}{2D_1} + \left(\frac{U^2}{4D_1} + \frac{V^2}{4D_2}\right)t\right]\left[N(t)/r \cosh (st) + P(t) \sinh (st)\right]$$

$$w_2(x,0,t) = \exp\left[-\frac{Ux}{2D_1} + \left(\frac{U^2}{4D_1} + \frac{V^2}{4D_2}\right)t\right]\left[-N(t) \sinh (st) - P(t)\, r \cosh (st)\right] \tag{3.19}$$

$$w_i(x,B,t) = 0$$

$$\text{or} \tag{3.20}$$

$$\operatorname*{Lt}_{y \to \infty} w_i(x,y,t) = 0 \; ; \; i = 1,2$$

(i) Finite habitat :

Solving (3.15) with conditions (3.16) - (3.20) in the case of a finite habitat ($0 < x < L$, $0 < y < B$) by using double Fourier finite sine transform with respect to x and y and then inverting the resulting solution with the help of (3.14),we get

$$v_i(x,y,t) = \frac{4D_2\pi}{LB^2} \exp\left[\frac{U}{2D_1}x + \frac{V}{2D_2}y\right] \cdot \tag{3.21}$$

$$\cdot \sum_{m=1}^{\infty} \sum_{n=1}^{\infty} n\, G_i(t)\, \theta(m) \sin\left(\frac{m\pi x}{L}\right) \sin\left(\frac{n\pi y}{B}\right); \; i=1,2$$

where,

$$G_i(t) = \int_0^t V_{i1}(T) \exp\left[-F_1(m,n)T\right] dT \tag{3.22}$$

$$F_1(m,n) = \frac{U^2}{4D_1} + \frac{V^2}{4D_2} + \frac{D_1 m^2\pi^2}{L^2} + \frac{D_2 n^2\pi^2}{B^2} \tag{3.23}$$

$$\theta(m) = \int_0^L \exp\left(-\frac{U}{2D_1}x\right) \sin\left(\frac{m\pi x}{L}\right) dx \tag{3.24}$$

$$V_{11}(T) = N(t)\cosh(sT) - P(t)r\sinh(sT)$$
$$V_{21}(T) = P(t)\cosh(sT) - N(t)/r\sinh(sT) \tag{3.25}$$

Keeping in view of (3.9) and (3.25) it can be noted that the finite limit of $v_i(x,y,t)$, $i = 1,2$ i.e. $v_i^s(x,y)$, exists provided

$$F_1(m,n) - s > 0 \tag{3.26}$$

and is given by

$$v_1^s(x,y) = \frac{4}{LB^2} \exp\left[\frac{U}{2D_1}x + \frac{V}{2D_2}y\right]$$

$$\sum_{m=1}^{\infty} \sum_{n=1}^{\infty} F_{11} \left[F_1(m,n)N_o - P_o f\right] \sin\left(\frac{m\pi x}{L}\right) \sin\left(\frac{n\pi y}{B}\right) \tag{3.27-a}$$

$$v_2^s(x,y) = \frac{4}{LB^2} \exp \left[\frac{U}{2D_1} x + \frac{V}{2D_2} y \right]$$

$$\sum_{m=1}^{\infty} \sum_{n=1}^{\infty} F_{11} \left[F_1(m,n)P_o - N_o g \right] \sin\left(\frac{m\pi x}{L}\right) \sin\left(\frac{n\pi y}{B}\right) \tag{3.27-b}$$

where

$$F_{11} = \left[F_1^2(m,n) - s^2 \right]^{-1}$$

It can be verified that (3.27) is also the steady state solution of the corresponding system leading to the asymptotic stability of the equilibrium state under the condition

$$\frac{U^2}{4D_1} + \frac{V^2}{4D_2} + \frac{D_1\pi^2}{L^2} + \frac{D_2\pi^2}{B^2} - s > 0 \tag{3.28}$$

obtained from (3.26) for $m = n = 1$.

It is pointed out here that the stability condition (3.28) is the same for both the constant and time dependent boundary conditions, provided (3.9) is satisfied.

Further, even if the condition (3.28) is not satisfied an equilibrium state would be asymptotically stable under the condition

$$N = Pr \tag{3.29}$$

to the corresponding steady state distribution given by

$$v_1^s(x,y) = \frac{4}{LB^2} \exp \left[\frac{Ux}{2D_1} + \frac{Vy}{2D_2} \right]$$

$$\sum_{m=1}^{\infty} \sum_{n=1}^{\infty} N_o \bar{F}_{11}(m,n) \sin\left(\frac{m\pi x}{L}\right) \sin\left(\frac{n\pi y}{B}\right) \tag{3.30-a}$$

$$v_2^s(x,y) = \frac{4}{LB^2} \exp\left[\frac{Ux}{2D_1} + \frac{Vy}{2D_2}\right]$$

$$\sum_{m=1}^{\infty} \sum_{n=1}^{\infty} P_o \bar{F}_{11}(m,n) \sin\left(\frac{m\pi x}{L}\right) \sin\left(\frac{n\pi y}{B}\right) \quad (3.30\text{-b})$$

where

$$\bar{F}_{11}(m,n) = \left[F_1(m,n) + s\right]^{-1} .$$

(ii) Semi-infinite habitat :

In the case of a semi-infinite habitat ($0 < x < L$, $0 < y < \infty$), the solution of the system (3.4) with initial and boundary conditions (3.5) - (3.10) can be obtained by taking first Fourier finite sine transform with respect to x and later Fourier sine transform with respect to y of the system (3.15) and then inverting with the help of (3.14), we get

$$v_i(x,y,t) = \frac{4D_2}{L\pi} \exp\left[\frac{Ux}{2D_1} + \frac{Vy}{2D_2}\right] .$$

$$\Sigma\ \theta\ (m) \int_0^t T^{-3/2}\ V_{i1}(T) \exp\left[-F_2(m)T - \frac{y^2}{4D_2 T}\right] dT \quad (3.31)$$

where

$$F_2(m) = \frac{U_1^2}{4D_1} + \frac{U_2^2}{4D_2} + \frac{D_1\ m^2\pi^2}{L^2} \quad (3.32)$$

As $t \to \infty$, it can be noted from (3.31) that the limit of $v_i(x,y,t)$ would exist provided

$$F_2(m) - s > 0 \quad (3.33)$$

and is given by

$$v_1^s(x,y) = \frac{2}{L} \exp\left[\frac{U}{2D_1}x + \frac{V}{2D_2}y\right] \sum_{m=1}^{\infty} \theta(m)\, \frac{1}{2} \left[(N_o - P_o r)\right.$$

$$\left. \exp\left(-\frac{\bar{F}_{12}y}{\sqrt{D_2}}\right) + (N_o + P_o r)\exp\left(-\frac{\bar{F}_{22}y}{\sqrt{D_2}}\right)\right] \sin\left(\frac{m\pi x}{L}\right) \tag{3.34}$$

$$v_2^s(x,y) = \frac{2}{L} \exp\left[\frac{U}{2D_1}x + \frac{V}{2D_2}y\right] \sum_{m=1}^{\infty} \theta(m)\, \frac{1}{2} \left[(P_o - N_o/r)\right.$$

$$\left. \exp\left(-\frac{\bar{F}_{12}y}{\sqrt{D_2}}\right) + (P_o + N_o/r)\exp\left(-\frac{\bar{F}_{22}y}{\sqrt{D_2}}\right)\right] \sin\left(\frac{m\pi x}{L}\right)$$

where

$$\bar{F}_{12}^2 = \frac{U^2}{4D_1} + \frac{V^2}{4D_2} + \frac{D_1 m^2 \pi^2}{L^2} - s \tag{3.35}$$

$$\bar{F}_{22}^2 = \frac{U^2}{4D_1} + \frac{V^2}{4D_2} + \frac{D_1 m^2 \pi^2}{L^2} + s \tag{3.36}$$

which are the same as the steady state solution showing the asymptotic stability of the equilibrium state under the condition

$$\frac{U^2}{4D_1} + \frac{V^2}{4D_2} + \frac{D_1 \pi^2}{L^2} - s > 0 \tag{3.37}$$

Again, in this case also the equilibrium state may become asymptotically stable under the condition (3.29) irrespective of the condition (3.37), to the steady state solution given by

$$v_1^s(x,y) = \frac{2}{L} \exp\left[\frac{Ux}{2D_1} + \frac{Vy}{2D_2}\right]$$

$$\sum_{m=1}^{\infty} \theta(m)\, N_o \exp\left[-\frac{f_{22}y}{\sqrt{D_2}}\right] \sin\left(\frac{m\pi x}{L}\right) \tag{3.38}$$

$$v_2^s(x,y) = \frac{2}{L} \exp\left[\frac{Ux}{2D_1} + \frac{Vy}{2D_2}\right]$$

$$\sum_{m=1}^{\infty} \theta(m)\, P_o \exp\left[-\frac{\bar{F}_{22}y}{\sqrt{D_2}}\right] \sin\left(\frac{m\pi x}{L}\right)$$

which is the same as (3.34) with (3.29) assuring the uniqueness of the steady-state.

3.3.2 UNEQUAL CONVECTION AND DISPERSION

Now consider the case

$$\frac{U_1}{D_{1x}} = \frac{U_2}{D_{2x}} \; ; \; \frac{V_1}{D_{1y}} = \frac{V_2}{D_{2y}} \tag{3.39}$$

which seems to be more realistic

Using the following transformation

$$v_i = w_i \exp\left(\frac{U_i}{2D_{ix}} x + \frac{V_i}{2D_{iy}} y\right); \; i = 1,2 \tag{3.40}$$

the system (3.4) reduces to

$$\frac{\partial w_1}{\partial t} = -ew_1 - fw_2 + D_{1x}\frac{\partial^2 w_1}{\partial x^2} + D_{1y}\frac{\partial^2 w_1}{\partial y^2}$$

$$\tag{3.41}$$

$$\frac{\partial w_2}{\partial t} = -gw_1 - hw_2 + D_{2x}\frac{\partial^2 w_2}{\partial x^2} + D_{2y}\frac{\partial^2 w_2}{\partial y^2}$$

where

$$e = \frac{U_1^2}{4D_{1x}} + \frac{V_1^2}{4D_{1y}}$$

$$h = \frac{U_2^2}{4D_{2x}} + \frac{V_2^2}{4D_{2y}} \tag{3.42}$$

(i) Finite habitat

The solution of the system (3.41) with initial and boundary conditions (3.5) - (3.10) under the transformation (3.40) can be obtained by using Laplace and double Fourier sine transforms with respect to t and x,y respectively from which the solution of the original system (3.4) can be written as follows :

$$v_1(x,y,t) = \frac{4\pi}{LB^2} \exp\left(\frac{U_1}{2D_{1x}} x + \frac{V_1}{2D_{1y}} y\right) \sum_{m=1}^{\infty} \sum_{n=1}^{\infty} \int_0^t \Big[A_{1mn} \exp(-p_{1mn}T) + B_{1mn} \exp(-p_{2mn}T)\Big] dT \sin\left(\frac{m\pi x}{L}\right) \sin\left(\frac{n\pi y}{B}\right)$$

$$v_2(x,y,t) = \frac{4\pi}{LB^2} \exp\left(\frac{U_2}{2D_{2x}} x + \frac{V_2}{2D_{2y}} y\right) \sum_{m=1}^{\infty} \sum_{n=1}^{\infty} \int_0^t \Big[A_{2mn} \exp(-p_{1mn}T) + B_{2mn} \exp(-p_{2mn}T)\Big] dT \sin\left(\frac{m\pi x}{L}\right) \sin\left(\frac{n\pi y}{B}\right) \tag{3.43}$$

where

$$A_{1mn} = \frac{D_{1y}(p_{1mn} - H_{mn})\,\bar{N}^*(m,t-T) + f\,D_{2y}\,\bar{P}^*(m,t-T)}{p_{1mn} - p_{2mn}}$$

$$B_{1mn} = \frac{D_{1y}(H_{mn} - p_{2mn})\,\bar{N}^*(m,t-T) - f\,D_{2y}\,\bar{P}^*(m,t-T)}{p_{1mn} - p_{2mn}} \tag{3.44-a}$$

$$A_{2mn} = \frac{D_{2y}(p_{1mn} - E_{mn})\,\bar{P}^*(m,t-T) + g\,D_{1y}\,\bar{N}^*(m,t-T)}{p_{1mn} - p_{2mn}}$$

$$B_{2mn} = \frac{D_{2y}(E_{mn} - p_{2mn})\,\bar{P}^*(m,t-T) - g\,D_{1y}\,\bar{N}^*(m,t-T)}{p_{1mn} - p_{2mn}} \qquad (3.44\text{-b})$$

$$p_{1mn},\ p_{2mn} = \frac{1}{2}\left[(E_{mn} + H_{mn}) \pm \sqrt{(E_{mn}-H_{mn})^2+4\,fg}\right] \qquad (3.45)$$

$$E_{mn} = e + D_{1x}\,\frac{m^2\pi^2}{L^2} + D_{1y}\,\frac{n^2\pi^2}{B^2}$$

$$H_{mn} = h + D_{2x}\,\frac{m^2\pi^2}{L^2} + D_{2y}\,\frac{n^2\pi^2}{B^2} \qquad (3.46)$$

$$\bar{N}^*(m,t) = N(t)\int_0^L \exp\left(-\frac{U_1}{2D_{1x}}\,x\right)\sin\left(\frac{m\pi x}{L}\right)dx$$

$$\bar{P}^*(m,t) = P(t)\int_0^t \exp\left(-\frac{U_2}{2D_{2x}}\,x\right)\sin\left(\frac{m\pi x}{L}\right)dx \qquad (3.47)$$

It can be noted from (3.43) that as $t \to \infty$, the limit of $v_i(x,y,t)$; $i = 1,2$ exist, provided

$$\left(\frac{U_1^2}{4D_{1x}} + \frac{V_1^2}{4D_{1y}} + \frac{D_{1x}\pi^2}{L^2} + \frac{D_{1y}\pi^2}{B^2}\right)\left(\frac{U_2^2}{4D_{2x}} + \frac{V_2^2}{4D_{2y}} + \frac{D_{2x}\pi^2}{L^2} + \frac{D_{2y}\pi^2}{B^2}\right) - s^2 > 0 \qquad (3.48)$$

and is given by

$$v_1^s(x,y) = \frac{4\pi}{LB^2}\exp\left(\frac{U_1}{2D_{1x}}\,x + \frac{V_1}{2D_{1y}}\,y\right)\sum_{m=1}^{\infty}\sum_{n=1}^{\infty} n\left[\frac{\bar{A}_{1mn}}{p_{1mn}} + \frac{\bar{B}_{2mn}}{p_{2mn}}\right]\sin\left(\frac{m\pi x}{L}\right)\sin\left(\frac{n\pi y}{B}\right) \qquad (3.49\text{-a})$$

$$v_2^s(x,y) = \frac{4\pi}{LB^2} \exp\left(\frac{U_2}{2D_{2x}} x + \frac{V_2}{2D_{2y}} y\right) \sum_{m=1}^{\infty} \sum_{n=1}^{\infty} \left[\frac{\bar{A}_{2mn}}{p_{1mn}} + \frac{\bar{B}_{2mn}}{p_{2mn}} \right]$$

$$\sin\left(\frac{m\pi x}{L}\right) \sin\left(\frac{n\pi y}{B}\right) \qquad (3.49\text{-b})$$

where $\bar{A}_{imn}$, $\bar{B}_{imn}$ are the same as A_{imn}, B_{imn} respectively with $N(t)$, $P(t)$ replaced by N_o, P_o. It is pointed out here that (3.49) is the same as the steady state solution of the corresponding system showing the asymptotic stability of the equilibrium state under the condition (3.48). The condition (3.48) is similar to (3.28) and in the special case of equal convection and dispersion these are same.

Further, even if (3.48) is not satisfied the equilibrium state may still be stable under (3.28).

(ii) Semi infinite habitat

In the case of semi-infinite habitat the solution of the system (3.41) is found by using Laplace transform with respect to t and Fourier sine transform with respect to x and y and then using the transformation (3.40), the final solution of the system (3.4) can be obtained as follows :

$$\bar{w}_1\ (x,y,p) = \frac{2}{D_{1y}\ D_{2y}\ L} \exp\left(\frac{U_1}{2D_{1x}}\ x\right) \sum_{m=1}^{\infty} \left[\bar{A}_{1m}(p) \exp\left(-q_{1m}^{1/2}\ y\right) + \bar{B}_{1m}(p) \exp\left(-q_{2m}^{1/2} y\right) \right] \sin\left(\frac{m\pi x}{L}\right) \tag{3.50}$$

$$\bar{w}_2\ (x,y,p) = \frac{2}{D_{1y}\ D_{2y}\ L} \exp\left(\frac{U_2}{2D_{2x}}\ x\right) \sum_{m=1}^{\infty} \left[\bar{A}_{2m}(p) \exp\left(-q_{2m}^{1/2}\ y\right) + \bar{B}_{2m}(p) \exp\left(-q_{2m}^{1/2} y\right) \right] \sin\left(\frac{m\pi x}{L}\right)$$

where

$$\bar{A}_{1m}(p) = \frac{N(p)\theta_1(m)D_{1y}\left(q_{1m}D_{2y}-p-h-D_{2x}\ \frac{m^2\pi^2}{L^2}\right) + f\ D_{2y}\ P(p)\ \theta_2(m)}{q_{1m} - q_{2m}}$$

$$\bar{B}_{1m}(p) = \frac{N(p)\theta_1(m)D_{1y}\left(p+h+D_{2x}\ \frac{m^2\pi^2}{L^2} - q_{2m}D_{2y}\right) - f\ D_{2y}\ P(p)\ \theta_2(m)}{q_{1m} - q_{2m}} \tag{3.51-a}$$

$$\bar{A}_{2m}(p) = \frac{P(p)\theta_2(m)D_{2y}\left(q_{1m}\ D_{1y}-p-e-D_{1x}\ \frac{m^2\pi^2}{L^2}\right) + g\ D_{1y}\ N(p)\ \theta_1(m)}{q_{1m} - q_{2m}}$$

$$\bar{B}_{2m}(p) = \frac{P(p)\theta_2(m)D_{2y}\left(p+e+D_{1x}\ \frac{m^2\pi^2}{L^2} - q_{2m}D_{1y}\right) - g\ D_{1y}\ N(p)\ \theta_1(m)}{q_{1m} - q_{2m}} \tag{3.51-b}$$

where

$$q_{1m}, q_{2m} = \frac{1}{2D_{1y}\ D_{2y}} \left[\left(p+e+D_{1x}\ \frac{m^2\pi^2}{L^2}\right)D_{2y} + \left(p+h+D_{2x}\ \frac{m^2\pi^2}{L^2}\right) D_{1y} \pm \left[\left\{ \left(p+e+D_{1x}\ \frac{m^2\pi^2}{L^2}\right)D_{2y} + \left(p+h+D_{2x}\ \frac{m^2\pi^2}{L^2}\right) D_{1y} \right\}^2 - 4\left\{ \left(p+e+D_{1x}\ \frac{m^2\pi^2}{L^2}\right)\left(p+h+D_{2x}\ \frac{m^2\pi^2}{L^2}\right) D_{1y}\ D_{2y} + fg \right\} \right]^{1/2} \right] \tag{3.52}$$

$$\theta_1(m) = \int_o^L \exp\left(-\frac{U_1}{2D_{1x}}x\right)\sin\left(\frac{m\pi x}{L}\right)dx$$

$$\theta_2(m) = \int_o^L \exp\left(-\frac{U_2}{2D_{2x}}x\right)\sin\left(\frac{m\pi x}{L}\right)dx \tag{3.53}$$

and N(p), P(p) denote the Laplace transforms N(t) and P(t) respectively.

To investigate the asymptotic behaviour of $v_i(x,y,t)$; $i = 1,2$ as $t \to \infty$, we use the following property of Laplace transform [See Le Page (1961) p. 315]

$$\underset{t \to \infty}{\mathrm{Lt}}\ v_i(x,y,t) = \underset{p \to 0}{\mathrm{Lt}}\ p\,\bar{v}_i(x,y,p) \tag{3.54}$$

Using (3.54) in (3.50) we get

$$v_1(x,y,t) = \frac{2}{D_{1y}\,D_{2y}\,L}\exp\left[\frac{U_1}{2D_{1x}}x + \frac{V_1}{2D_{1y}}y\right]$$

$$\sum_{m=1}^{\infty}\left[\frac{N_o\theta_1(m)D_{1y}(q^o_{1m}D_{2y}-h-D_{2x}\frac{m^2\pi^2}{L^2}) + f\,D_{2y}\,P_o\,\theta_2(m)}{q^o_{1m} - q^o_{2m}}\cdot\right.$$

$$\exp\left[-(q^o_{1m})^{1/2}y\right] + \frac{N_o\theta_1(m)D_{1y}(h+D_{2x}\frac{m^2\pi^2}{L^2} - q^o_{2m}D_{2y}) - fD_{2y}P_o\theta_2(m)}{q^o_{1m} - q^o_{2m}}$$

$$\left.\exp\left[-(q^o_{2m})^{1/2}y\right]\right]\sin\left(\frac{m\pi x}{L}\right) \tag{3.55-a}$$

$$v_2(x,y,t) = \frac{2}{D_{1y}\, D_{2y}\, L} \exp\left[\frac{U_2}{2D_{2x}} x + \frac{V_2}{2D_{2y}} y\right]$$

$$\sum_{m=1}^{\infty}\left[\frac{P_o\theta_2(m)D_{2y}(q^o_{1m}D_{1y} - e - D_{1x}\frac{m^2\pi^2}{L^2}) + g\, D_{1y}\, N_o\, \theta_1(m)}{q^o_{1m} - q^o_{2m}}\right.$$

$$\cdot \exp\left[q^o_{1m})^{1/2}\, y\right]$$

$$+ \frac{P_o\theta_2(m)D_{2y}(e + D_{1x}\frac{m^2\pi^2}{L^2} - q^o_{2m}\, D_{1y}) - g\, D_{1y}\, N_o\, \theta_1(m)}{q^o_{1m} - q^o_{2m}}$$

$$\exp\left[-(q^o_{2m})^{1/2}\, y\right] \sin\left(\frac{m\pi x}{L}\right) \qquad (3.55\text{-b})$$

which would exist provided

$$\left(\frac{U_1^2}{4D_{1x}} + \frac{V_1^2}{4D_{1y}} + \frac{D_{1x}\pi^2}{L^2}\right)\left(\frac{U_2^2}{4D_{2x}} + \frac{V_2^2}{4D_{2y}} + \frac{D_{2x}\pi^2}{L^2}\right) - s^2 > 0 \qquad (3.56)$$

where q^o_{1m}; $i = 1,2$ is calculated from (3.52) at $p = 0$.

For equal convection and dispersion the condition for stability (3.56) is the same as (3.37). Further, even if the condition (3.56) is not satisfied the equilibrium state may be stable under condition (3.29) also.

3.4 COMPETITION MODEL UNDER ZERO LONGITUDINAL DISPERSION

In the previous article, we have studied the linear stability of competition model for nonzero dispersion coefficients. However, it may be noted here that the transformation (3.14) and the solutions thus obtained are not valid for $D_1(\bar{u}_1,\bar{u}_2) = 0$ or $D_2(\bar{u}_1,\bar{u}_2) = 0$ when $U_1 \neq 0$ or $U_2 \neq 0$. Therefore, to understand the behaviour of the solution insuch cases, in the following we discuss the stability of the system when $D_1 = 0$ or $D_2 = 0$.

This case is applicable when the dispersive migration in a particular direction is zero due to dense population of the species arising out of non-homogeneity of habitat or when the convective migration is dominant over dispersion in that particular direction.

In the following the stability of equilibrium state is discussed for the case of equal convection and dispersion for two species when $D_{1x} = D_{2x} = 0$.

(i) Finite habitat

Using the transformation

$$X = \exp\left[\frac{Vy}{2D} - \frac{V^2 t}{4D}\right] AX_1$$

$$X_1 = \exp\left[\frac{V^2 t}{4D} - \frac{Vy}{2D}\right] A^{-1} X \tag{3.57}$$

the solution of the system (3.4) is obtained under initial and boundary conditions (3.5) - (3.10) as

$$v_i(x,y,t) = \frac{2D\pi}{L^2} \exp\left(\frac{Vy}{2D}\right) \sum_{m=1}^{\infty} m\, G_i'(t) \sin\left(\frac{m\pi x}{L}\right); \quad t < x/U \tag{3.58}$$

$$v_i(x,y,t) = \frac{2D\pi}{L^2} \exp\left(\frac{Vy}{2D}\right) \sum_{m=1}^{\infty} m\, \bar{G}_i'(t) \sin\left(\frac{m\pi x}{L}\right); \quad t > x/U \tag{3.59}$$

for $i = 1,2$

where

$$G_i'(a) = \int_0^a V_{i1}(T) \exp\left[-F_1'(m)T\right] dT \tag{3.60}$$

$$\bar{G}_i'(a) = 1/U \int_0^a V_{i1}(T/U) \exp\left[-\frac{F_1'(m)T}{U}\right] dT \tag{3.61}$$

$$F_1'(m) = \frac{Dm^2\pi^2}{L^2} + \frac{V^2}{4D} . \tag{3.62}$$

We discuss the following two cases :

Case 1 : $U = 0$. In this case the population densities $v_i(x,y,t)$, $i = 1,2$ is given by (3.58) and, as before, its limit as $t \to \infty$ can exist provided

$$F_1'(m) - s > 0 \tag{3.63}$$

is satisfied and can be obtained as

$$\begin{aligned} v_1^s(x,y) &= \frac{2D\pi}{L^2} \exp\left(\frac{Vy}{2D}\right) \\ &\quad \sum_{m=1}^{\infty} m\, F_{11}'(m) \left[F_1'(m)\, N_o - fP_o\right] \sin\left(\frac{m\pi y}{B}\right) \\ v_2^s(x,y) &= \frac{2D\pi}{L^2} \exp\left(\frac{Vy}{2D}\right) \\ &\quad \sum_{m=1}^{\infty} mF_{11}'(m) \left[F_1'(m) P_o - fN_o\right] \sin\left(\frac{m\pi y}{B}\right) \end{aligned} \tag{3.64}$$

where

$$F_{11}'(m) = \left[F_1'^2(m) - s^2\right]^{-1} .$$

It can be noted that (3.64) is also the steady state solution of the corresponding system showing the asymptotic stability of the equilibrium state under the condition

$$\frac{V^2}{4D} + \frac{D\pi^2}{L^2} - s > 0 \tag{3.65}$$

Comparing the conditions (3.28) and (3.65) it is also seen that the condition (3.65) is a one dimensional version of (3.28). Thus, it can be concluded that the equilibrium state which is stable in two dimensional habitat may not be stable in one dimensional habitat.

Further, even if the condition (3.65) is not satisfied the equilibrium state is stable under the condition (3.29) and the limiting solution obtained as $t \to \infty$ is the same as the steady state solution of the system, given by

$$v_1^s(x,y) = \frac{2D\pi}{L^2} \exp\left(\frac{V}{2D} y\right) \sum_{m=1}^{\infty} m \, N_o \, \bar{F}'_{11}(m) \sin\left(\frac{m\pi y}{B}\right)$$

$$v_2^s(x,y) = \frac{2D\pi}{L^2} \exp\left(\frac{V}{2D} y\right) \sum_{m=1}^{\infty} m \, P_o \bar{F}'_{11}(m) \sin\left(\frac{m\pi y}{B}\right) \tag{3.66}$$

where

$$\bar{F}'_{11}(m) = \left[F'_1(m) + s\right]^{-1}.$$

If none of the conditions (3.65) and (3.29) is satisfied then the equilibrium state is unstable.

Case 2 : $U \neq 0$. In this case the distribution of species as $t \to \infty$ is given by (3.59) and it is the same as the steady state solution of the corresponding system showing that, in the absence of longitudinal dispersion, the equilibrium state is always stable with convection in that direction.

(ii) Semi-infinite habitat

In the case of infinite habitat the distribution of the species are obtained as follows :

$$v_i(x,y,t) = \int_0^t V_{i1}(T)\,\bar{\phi}(x,y,T)\,dT, \quad t < x/U \tag{3.67}$$

$$v_i(x,y,t) = \int_0^x V_{i1}(Z/U_1)\,\bar{\psi}(x,y,Z)\,dZ, \quad t > x/U \tag{3.68}$$

$$i = 1,2$$

where

$$\bar{\phi}(x,y,T) = \frac{y}{2\sqrt{\pi D}}\, T^{-3/2} \exp\left[\frac{V}{2D}\, y - \frac{V^2}{4D}\, T - \frac{y^2}{4DT}\right] \tag{3.69}$$

$$\bar{\psi}(x,y,Z) = \frac{y}{2\sqrt{\frac{\pi D}{U}}}\, Z^{-3/2} \exp\left[\frac{V}{2D}\, y - \frac{V^2 Z}{4DU} - \frac{y^2 U}{4DZ}\right] \tag{3.70}$$

In the case U = 0, the finite limits of v_1, v_2, given by (3.67), as $t \to \infty$ can be obtained as

$$\begin{aligned} v_1^s(y) &= N_o \exp\left[-\left(\frac{V^2}{4D^2} + \frac{s}{D}\right)^{1/2} y\right] \\ v_2^s(y) &= P_o \exp\left[-\left(\frac{V^2}{4D^2} + \frac{s}{D}\right)^{1/2} y\right] \end{aligned} \tag{3.71}$$

provided condition (3.29) is satisfied. Further, the distribution (3.71) is the same as the steady state solution of the system (3.4) under (3.29) showing the asymptotic stability of the equilibrium state. It may be noted that the condition (3.29) is also needed for the existence of the steady state solution of the system (3.4) under boundary conditions (3.6) - (3.10).

Comparing this case ($D_1 = 0$), with $D_1 \neq 0$ in infinite habitat case, it can be seen that (3.29) is not needed for the existence of the steady state solution. Further, the case (i.e. $D_1 = 0$), stability of the equilibrium state (in the absence of longitudinal convection) remains unaffected by the presence of transverse convection and dispersion while for $D_1 \neq 0$, the transverse convection and dispersion have stabilizing effect.

Again, for $U_1 \neq 0$, it can be noted from (3.68) that the equilibrium state is always asymptotically stable to the steady state solution.

3.5 PREY PREDATOR MODEL

In the case of prey predator model, the interaction function f_i, $i = 1,2$ is prescribed as follows :

$$
\begin{aligned}
f_1 &= u_1(a_1 - c_1u_2) \\
f_2 &= u_2(-a_2 + c_2u_1)
\end{aligned}
\tag{3.72}
$$

The linearized system for the evolution of two species would be given by (3.4) with

$$
\begin{aligned}
b_{ii} &= 0 \\
b_{12} &= -f < 0 \\
b_{21} &= g > 0
\end{aligned}
\tag{3.73}
$$

The solution of the system (3.4) with (3.73) under conditions (3.5) - (3.10) in both finite and infinite habitats

for $D_1 = 0$ or $D_1 \neq 0$, are given by respective solutions in the case of competition model where s^2 is replaced by $-s^2$.

Noting (3.73) it can be seen from the solutions of the system in various cases that the equilibrium state which is otherwise neutrally stable is always asymptotically stable with convection and dispersion giving nonuniform spatial patterns.

3.6 CONCLUSIONS

The linear stability of two interacting species system in two dimensional habitats has been investigated by considering dispersive and convective migration of the species under time dependent boundary conditions. It has been shown that condition for stability of the equilibrium state under time dependent boundary conditions is the same as for constant boundary conditions if (3.9) is satisfied.

The following conclusions may be drawn from the analysis for the competition model.

1. In the case of a infinite habitat for D_1, D_2 nonzero, it has been shown that the equilibrium state may become stable with dispersion and convection in a two dimensional habitat provided (3.28) is satisfied.

2. Even if the condition (3.28) is not satisfied the equilibrium state is stable under the condition (3.29) involving the boundary conditions.

3. The equilibrium state which is stable under the condition (3.28) in the case of finite habitat may not be stable in the case of semi-infinite habitat because (3.37) may not be satisfied.

4. The equilibrium state is always stable with $U_1 \neq 0$ and $D_1 = 0$ in both finite and semi-infinite habitats.

5. It is noted from condition (3.28) and (3.65) that the equilibrium state which is stable in one dimensional finite habitat would stablize further in two dimensional finite habitat due to convection and dispersion in both longitudinal and transverse directions.

6. In semi-infinite habitat for $D_1 = U_1 = 0$ it has been shown that stability of the equilibrium state is unaffected by transverse convection and dispersion.

In the case of prey predator model the equilibrium state is always stable with dispersion and convection in all cases.

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CHAPTER IV

EFFECTS OF DISPERSION ON THE LINEAR STABILITY OF TWO SPECIES SYSTEM IN A TWO-DIMENSIONAL PATCHY HABITAT

4.1 INTRODUCTION

Though the mathematical modelling of interacting populations in a habitat has become quite sound after the work of Lotka and Volterra, it is only recently that the environmental and ecological effects have been considered on their evolutionary processes (Skellam, 1951 ; Segal and Jackson, 1972; Hadelar, 1974 ; Gopalsamy, 1977 ; Kerner, 1959) . Generally these effects are taken into account by identifying species migration with dispersive and convective processes which might have continuously varying properties due to environmental and ecological gradients in the habitat (Levin, 1974 ; Comins and Blatt, 1971). Although it has been pointed out by many workers (Huffaker, 1958, 1963; Comins and Blatt, 1974; Levin, 1974 ; Kawasaki et al, 1979) that migration of species may depend upon densities as well as location of the species, little attempt has been made to study such effects on the stability of population models. In such a case, not only the interaction terms but also the migration terms become nonlinear in the model and it is difficult to study such a system.

One approach to study such a problem is to divide the habitat into finitely many sub-habitats (patches)where the

dispersion coefficients may be assumed to be constants with values different in different patches. This method, though not exact, can give fairly close approximations as regards to the effects of dispersive migration on the evolution and coexistence of the species (Levin, 1974; Kawasaki et al, 1979).

In this chapter therefore, we study the effects of dispersive migration on the linear stability of two interacting species system in a two dimensional patchy habitat by following the above mentioned approach. Though the space dependence of interaction rates in the model would give greater realism, it would undully complicate the interpretation of the results and hence in this and in the following chapters these parameters have been assumed to be the same in all patches (Comins and Blatt, 1974). To see the importance of dispersive migration, the particular case of Volterra type competition model has been investigated in detail as the equilibrium state in this case is inherently unstable.

4.2 BASIC EQUATIONS

Consider the evolution of two interacting and migrating species in a two-dimensional heterogeneous habitat $[0 \leq x \leq L, 0 \leq y \leq B]$. Identifying the migration of the species. by dispersion process depending upon the density gradients of the species, the governing system for the evolution of species can be written as,

$$\frac{\partial u_i}{\partial t} = f_i(u_1,u_2) + \frac{\partial}{\partial x}\left[D_{ix}(x,y)\frac{\partial u_i}{\partial x}\right] + \frac{\partial}{\partial y}\left[D_{iy}(x,y)\frac{\partial u_i}{\partial y}\right] \tag{4.1}$$

where $u_i(x,y,t)$ is the density of the ith species at any point (x,y) and at any instant t. The terms $f_i(u_1,u_2)$, $i=1,2$ are due to the interaction of the species and (D_{ix},D_{iy}) denotes the dispersion coefficient of the ith species and may vary with space.

As pointed out earlier, divide the habitat into finitely many patches, say N, such that the dispersion in each patch is constant. Let jth patch be defined as $L_{j-1} < x \leq L_j$, $j=1,2,\ldots N$ with $L_o = 0$ and $L_N = L$. If u_{ij}, (D_{ijx},D_{ijy}) denote the density and dispersion coefficient of the ith species in the jth patch, the evolution of ith species in jth patch can then be written, from (4.1), as

$$\frac{\partial u_{ij}}{\partial t} = f_{ij} + D_{ijx}\frac{\partial^2 u_{ij}}{\partial x^2} + D_{ijy}\frac{\partial^2 u_{ij}}{\partial y^2}\ ;\ L_{j-1} < x < L_j$$

$$i=1,2,;\ j=1,2,\ldots N \tag{4.2}$$

Since it has been assumed that the interaction of the species remains unaffected by the patchiness of the habitat the nontrivial positive equilibrium state $(\bar{u}_{1j}, \bar{u}_{2j})$ of the above system can be obtained by solving

$$f_{ij} = 0\ ;\quad i=1,2,;\quad j=1,2,\ldots N$$

which are the same in all the patches i.e. $\bar{u}_{ij} = \bar{u}_i$.

The system (4.2) can be linearized by writing

$$u_{ij} = \bar{u}_i + v_{ij} \; ; \; i=1,2; \; j=1,2,\ldots,N$$

and neglecting square and higher order terms to get

$$\frac{\partial v_{ij}}{\partial t} = \sum_{k=1}^{2} b_{ik} v_{kj} + D_{ijx} \frac{\partial^2 v_{ij}}{\partial x^2} + D_{ijy} \frac{\partial^2 v_{ij}}{\partial y^2} \qquad (4.3)$$

where

$$b_{ik} = \left(\frac{\partial f_{ij}}{\partial u_{kj}}\right)_{\bar{u}_1, \bar{u}_2}$$

and v_{ij}, $i=1,2$; $j=1,2,\ldots N$ are the small perturbations about the equilibrium state.

The following initial, boundary and matching conditions may be associated with the above system.

Initial conditions :

$$v_{ij}(x,y,0) = G_{ij}(x) \; ; \; L_{j-1} < x \leq L_j \qquad (4.4\text{-a})$$

delete.

such that

$$G_{i(j-1)}(L_j) = G_{ij}(L_j); \; j=1,2,\ldots N \qquad (4.4\text{-b})$$

The equation (4.4-b) gives the matching of initial conditions at the jth interface.

Boundary conditions : The boundary conditions may be any of the following types:

1. Reservoir conditions

$$
\left.\begin{aligned}
v_{i1}(0,y,t) &= 0 \\
v_{iN}(L,y,t) &= 0 \\
v_{ij}(x,0,t) &= 0 \\
v_{ij}(x,B,t) &= 0
\end{aligned}\right\} \quad \begin{aligned} &i=1,2 \\ &j=1,2,\ldots N \end{aligned} \qquad (4.5\text{-a})
$$

2. Flux conditions:

$$\frac{\partial v_{i1}}{\partial x} = 0 \quad \text{at} \quad x = 0$$

$$\frac{\partial v_{iN}}{\partial x} = 0 \quad \text{at} \quad x = L \quad ; \; i=1,2; \; j=1,2\ldots N \qquad (4.5\text{-b})$$

$$\frac{\partial v_{ij}}{\partial x} = 0 \quad \text{at} \quad y = 0,\ B$$

3. Mixed conditions :

$$v_{i1}(0,y,t) = 0$$

$$v_{iN}(L,y,t) = 0 \qquad (4.5\text{-c})$$

$$\frac{\partial v_{ij}}{\partial y} = 0 \quad \text{at} \quad y=0,\ B \quad \text{for} \quad i=1,2;\; j=1,2\ldots N$$

or

$$\frac{\partial v_{i1}}{\partial x} = 0 \quad \text{at} \quad x=0$$

$$\frac{\partial v_{iN}}{\partial x} = 0 \quad \text{at} \quad x=L \qquad (4.5\text{-d})$$

$$v_{ij}(x,0,t) = 0 \qquad i=1,2 \;;\; j=1,2,\ldots N$$

$$v_{ij}(x,B,t) = 0$$

Matching conditions : Keeping in view of the continuity of species densities and fluxes at the interface of $(j-1)^{th}$ and j^{th} patches $j=2,3,\ldots N$ the matching conditions are

$$v_{i(j-1)}(L_{j-1},y,t) = v_{ij}(L_j,y,t) \tag{4.6}$$

$$D_{i(j-1)x}\frac{\partial v_{i(j-1)}}{\partial x} = D_{ijx}\frac{\partial v_{ij}}{\partial x} \text{ at } x=L_j \tag{4.7}$$

for $i=1,2,\ ;\ j=2,3,\ldots N.$

Now in the following the linear stability of Volterra type competition and prey predator interaction models have been discussed.

4.3 COMPETITION MODEL

The volterra interaction function for the competing species is given as follows:

$$\begin{aligned} f_1(u_1,u_2) &= u_1(a_1-c_1u_2) \\ f_2(u_1,u_2) &= u_2(a_1-c_2u_1) \end{aligned} \tag{4.8}$$

and the linearized system corresponding to (4.2) can be obtained from (4.3) as follows:

$$\begin{aligned} \frac{\partial v_{1j}}{\partial t} &= -fv_{2j} + D_{1jx}\frac{\partial^2 v_{1j}}{\partial x^2} + D_{1jy}\frac{\partial^2 v_{1j}}{\partial y^2}\ ;\ L_{j-1}<x\leq L_j, \\ & \qquad j=1,2,\ldots N \\ \frac{\partial v_{2j}}{\partial t} &= -gv_{1j} + D_{2jx}\frac{\partial^2 v_{2j}}{\partial x^2} + D_{2jy}\frac{\partial^2 v_{2j}}{\partial y^2} \end{aligned} \tag{4.9}$$

where $f = c_1a_2/c_2$; $g = c_2a_1/c_1$.

It may be noted that these equations are of reaction diffusion type which are linear and coupled. To reduce them into diffusion equation, the following transformation is used.

$$\begin{bmatrix} v_{1j} \\ v_{2j} \end{bmatrix} = \begin{bmatrix} r\cosh(st) & \sinh\ (st) \\ -\sinh\ (st) & -1/r\cosh(st) \end{bmatrix} \begin{bmatrix} z_{1j} \\ z_{2j} \end{bmatrix}; \quad j=1,2,\ldots N \tag{4.10}$$

where

$$r = \sqrt{f/g} \quad ; \quad s = \sqrt{fg}$$

The system (4.9), in transformed form, can be written as,

$$\frac{\partial z_{ij}}{\partial t} = D_{ijx}\frac{\partial^2 z_{ij}}{\partial x^2} + D_{ijy}\frac{\partial^2 z_{ij}}{\partial y^2} \quad i=1,2;\ j=1,2,\ldots N$$

$$L_{j-1} < x \leq L_j \tag{4.11}$$

The transformed initial and matching conditions are

$$\begin{aligned} z_{1j}(x,y,0) &= rG_1(x) \\ z_{2j}(x,y,0) &= -G_2(x)/r \end{aligned} \tag{4.12}$$

and

$$z_{i(j-1)}(L_j,y,t) = z_{ij}(L_j,y,t) \tag{4.13}$$

$$D_{i(j-1)x}\frac{\partial z_{i(j-1)}}{\partial x} = D_{ijx}\frac{\partial z_{ij}}{\partial x} \quad \text{at} \quad x=L_j \tag{4.14}$$

while the transformed boundary conditions would be given by (4.5) with v_{ij} replaced by z_{ij}.

4.3.1 DISCUSSION OF STABILITY UNDER RESERVOIR CONDITIONS

Solving the system (4.11) under zero reservoir boundary conditions, initial conditions (4.12) and matching conditions (4.13) and (4.14) we get

$$z_{1j}(x,y,t) = \sum_{m=1}^{\infty} \sum_{n=1}^{\infty} C_{mn} F_{mnj}(x) \sin\left(\frac{n\pi y}{B}\right) \exp\left(-\lambda_{mn}^{2} t\right) \qquad (4.15)$$

$$z_{2j}(x,y,t) = \sum_{m=1}^{\infty} \sum_{n=1}^{\infty} C'_{mn} F'_{mnj}(x) \sin\left(\frac{n\pi y}{B}\right) \exp\left(-\lambda'^{2}_{mn} t\right) \qquad (4.16)$$

where

$$F_{mn1}(x) = \frac{\sin\left(\frac{\lambda_{mn1} x}{\sqrt{D_{11x}}}\right)}{\sin\left(\frac{\lambda_{mn1} L_1}{\sqrt{D_{11x}}}\right)} \qquad (4.17\text{-a})$$

$$F_{mnj}(x) = \cos\left[\frac{\lambda_{mnj}(x-L_{j-1})}{\sqrt{D_{1jx}}}\right] F_{mn(j-1)}(L_{j-1}) \qquad (4.17\text{-b})$$

$$+ \frac{D_{1(j-1)x}}{\sqrt{D_{1jx}}\,\lambda_{mnj}} \sin\left[\frac{\lambda_{mnj}(x-L_{j-1})}{\sqrt{D_{1jx}}}\right] \frac{d}{dx}\left[F_{mn(j-1)}(x)\right]_{x=L_{j-1}}$$

$$F'_{mn1}(x) = \frac{\sin\left(\frac{\lambda'_{mn1} x}{\sqrt{D_{21x}}}\right)}{\sin\left(\frac{\lambda'_{mn1} L_1}{\sqrt{D_{21x}}}\right)} \qquad (4.18\text{-a})$$

$$F'_{mnj}(x) = \cos\left[\frac{\lambda'_{mnj}(x-L_{j-1})}{\sqrt{D_{2jx}}}\right] F'_{mn(j-1)}(L_{j-1})$$

$$+ \frac{D_{2(j-1)x}}{\sqrt{D_{2jx}}\ \lambda'_{mnj}} \sin\left[\frac{\lambda'_{mnj}(x-L_{j-1})}{\sqrt{D_{2jx}}}\right] \tag{4.18-b}$$

$$\frac{d}{dx}\left[F'_{mn(j-1)}(x)\right]_{x=L_{j-1}}$$

$$\lambda^2_{mnj} = \lambda^2_{mn} - D_{1jy}\frac{n^2\pi^2}{B^2} \tag{4.19}$$

$$\lambda'^2_{mnj} = \lambda'^2_{mn} - D_{2jy}\frac{n^2\pi^2}{B^2}$$

$$C_{mn} = \frac{\int_0^L\int_0^B z_1(x,y,0)\ F_{mn}(x)\ \sin(\frac{n\pi y}{B})\ dxdy}{||F_{mn}(x)\ \sin\ (\frac{n\pi y}{B})||} \tag{4.20-a}$$

$$C'_{mn} = \frac{\int_0^L\int_0^B z_2(x,y,0)\ F'_{mn}(x)\ \sin\ (\frac{n\pi y}{B})\ dxdy}{||F'_{mn}(x)\ \sin(\frac{n\pi y}{B})||} \tag{4.20-b}$$

$$||A||^2 = \int_0^L\int_0^B A^2\ dx\ dy$$

and λ_{mn}, λ'_{mn} are the roots of the following equations, obtained by using zero boundary conditions at the end $x=L$ in (4.16) with (4.18-b) for $j=N$.

$$\frac{D_{1(N-1)x}}{D_{1Nx}} + \frac{\lambda_{mnN}\ F_{mn(N-1)}(L_{N-1})}{\sqrt{D_{1Nx}}\ \frac{d}{dx}\left[F_{mn(N-1)}(x)\right]_{x=L_{N-1}}} \cot\left[\frac{\lambda_{mnN}(L-L_{N-1})}{\sqrt{D_{1Nx}}}\right]=0$$

(4.21-b)

$$\frac{D_{2(N-1)x}}{D_{2Nx}} + \frac{\lambda'_{mnN}\, F'_{mn(N-1)}(L_{n-1})}{\sqrt{D_{2Nx}}\, \frac{d}{dx}\left[F'_{mn(N-1)}(x)\right]_{x=L_{N-1}}} \cdot \cot\left[\frac{\lambda'_{mnN}(L-L_{N-1})}{\sqrt{D_{2Nx}}}\right] = 0$$

(4.21-b)

respectively. Substitution of (4.21-a) in (4.17-b) for $j = N$ gives,

$$F_{mnN}(x) = \frac{F_{mn(N-1)}(L_{N-1})}{\sin\left[\frac{\lambda_{mnN}(L-L_{N-1})}{\sqrt{D_{1Nx}}}\right]} \cdot \sin\left[\frac{\lambda_{mnN}(x-L_{N-1})}{\sqrt{D_{1Nx}}}\right] \qquad (4.22)$$

Similar expression for $F'_{mnN}(x)$ is also obtained.

Using the transformation (4.10), the final solution of the original system (4.9) can be obtained as follows :

$$v_{1j}(x,y,t) = \sum_{m=1}^{\infty}\sum_{n=1}^{\infty}\Big[C_{mn}\, F_{mnj}(x)\, r \cosh(st) \exp(-\lambda_{mn}^2 t)$$

$$+ C'_{mn}\, F'_{mnj}(x) \sinh(st) \exp(-\lambda'^2_{mn}\, t)\Big] \sin\left(\frac{n\pi y}{B}\right)$$

(4.23)

$$v_{2j}(x,y,t) = \sum_{m=1}^{\infty}\sum_{n=1}^{\infty} -\Big[C_{mn}\, F_{mnj}(x) \sinh(st) \exp(-\lambda_{mn}^2\, t)$$

$$+ C'_{mn}\, F'_{mnj}(x) \frac{\cosh(st)}{r} \exp(-\lambda'^2_{mn}\, t)\Big] \sin\left(\frac{n\pi y}{B}\right)$$

It can be noted from (4.23) that the finite limit of v_{ij}; $i = 1,2$; $j = 1,2,\ldots,N$ as $t \to \infty$ would exist provided

$$\lambda_{mn}^2 - s > 0$$

$$\lambda'^2_{mn} - s > 0 \qquad (4.24)$$

which are combined to give the following condition for stability

$$\lambda_{11}^2 \ \lambda_{11}'^2 - s^2 > 0 \qquad (4.25)$$

where λ_{11}, λ'_{11} denote the minimum values of λ_{mn}, λ'_{mn} respectively. It can be noted that zero values of λ_{11}, λ'_{11} are also the solution of (4.21) giving trivial solution in (4.23) and hence λ_{11}, λ'_{11} are taken to be nonzero. Thus, the equilibrium state under the condition (4.25) is asymptotically stable to the steady state solution (zero solution).

It can also be noted from (4.23) that the condition (4.25) is common for all patches and thus stability in a particular patch not only depends upon the dispersion coefficient and length of this patch but on other patches also.

To see the effects of dispersion on the stability of the equilibrium state more precisely, we consider the particular cases of habitats with two and three patches only. In case of two patches the equations (4.21) determining λ_{mn} and λ'_{mn} reduce to the following form

$$\lambda_{mn1} \cot \left[\frac{\lambda_{mn1} L_1}{\sqrt{D_{11x}}}\right] + \sqrt{\frac{D_{12x}}{D_{11x}}} \ \lambda_{mn2} \cot \left[\frac{\lambda_{mn2}(L-L_1)}{\sqrt{D_{12x}}}\right] = 0 \qquad (4.26\text{-a})$$

$$\lambda'_{mn1} \cot \left[\frac{\lambda'_{mn1} L_1}{\sqrt{D_{21x}}}\right] + \sqrt{\frac{D_{22x}}{D_{21x}}} \ \lambda'_{mn2} \cot \left[\frac{\lambda'_{mn2}(L-L_1)}{\sqrt{D_{22x}}}\right] = 0 \qquad (4.26\text{-b})$$

For equal dispersion coefficients in y directions, it can be noted from (4.19) that

$$\lambda^2_{mn1} = \lambda^2_{mn2} = \bar{\lambda}^2_{mn}$$

$$\lambda'^2_{mn1} = \lambda'^2_{mn2} = \bar{\lambda}'^2_{mn}$$

reducing the equation (4.26) to

$$\cot\left[\frac{\bar{\lambda}_{mn}L_1}{\sqrt{D_{11x}}}\right] + \sqrt{\frac{D_{12x}}{D_{11x}}}\cot\left[\frac{\bar{\lambda}_{mn}(L-L_1)}{\sqrt{D_{12x}}}\right]=0 \qquad (4.27)$$

and similar equation for λ'_{mn} can also be written from (4.26-b).

In case of three patches, the equation (4.21) for equal dispersion coefficients in y directions, gives

$$\sqrt{\frac{D_{12x}}{D_{13x}}} + \cot\left[\frac{\bar{\lambda}_{mn}(L-L_2)}{\sqrt{D_{13x}}}\right].$$

$$\frac{\sqrt{D_{11x}}\cos\left[\frac{\bar{\lambda}_{mn}L_1}{\sqrt{D_{11x}}}\right]\sin\left[\frac{\bar{\lambda}_{mn}(L_2-L_1)}{\sqrt{D_{12x}}}\right]+\sqrt{D_{12x}}\cos\left[\frac{\bar{\lambda}_{mn}(L_2-L_1)}{\sqrt{D_{12x}}}\right]\sin\left[\frac{\bar{\lambda}_{mn}L_1}{\sqrt{D_{11x}}}\right]}{\sqrt{D_{11x}}\cos\left[\frac{\bar{\lambda}_{mn}L_1}{\sqrt{D_{11x}}}\right]\cos\left[\frac{\bar{\lambda}_{mn}(L_2-L_1)}{\sqrt{D_{12x}}}\right]-\sqrt{D_{12x}}\sin\left[\frac{\bar{\lambda}_{mn}L_1}{\sqrt{D_{11x}}}\right]\sin\left[\frac{\bar{\lambda}_{mn}(L_2-L_1)}{\sqrt{D_{12x}}}\right]} = 0 \qquad (4.28)$$

and similar equation for $\bar{\lambda}'_{mn}$ can also obtained from Equation (4.27) is solved numerically for the minimum root $\bar{\lambda}_{11}$ of $\bar{\lambda}_{mn}$ and it is plotted in figure 1 for various values

of $\bar{D}_2 = \sqrt{\frac{D_{12x}}{D_{11x}}}$ and D_{11x}, L_1/L being fixed. It is clear from figure 1 that $\bar{\lambda}_{11}$ increases with $\bar{D}_2$ for all values of L_1/L and this increase in $\bar{\lambda}_{11}$ is enhanced as L_1/L decreases for $\bar{D}_2 > 1$ but reverse is the case when $\bar{D}_2 < 1$.

Again equation (4.28) is solved numerically and the graph is plotted in figure 2 between $\bar{\lambda}_{11}$ and $\bar{D}_3 = \sqrt{\frac{D_{13x}}{D_{11x}}}$ from which it can be noticed that $\bar{\lambda}_{11}$ increases with $\bar{D}_3$ for fixed $\bar{D}_2$, L_1/L, L_2/L. Further, the increase in λ_{11} enhances with L_2/L for $\bar{D}_3/\bar{D}_2 > 1$ for fixed L_1/L while opposite is the case for $\bar{D}_3/\bar{D}_2 < 1$.

By induction, it can be argued that these results are valid for habitats with finitely many patches also.

Thus, keeping in view of the condition (4.25) and expression (4.23) it can be seen that convergence of unsteady state solution to the zero steady state solution increases as the dispersion in the patchy habitat increases. In other words the degree of the stability of the equilibrium state increases with dispersion.

4.3.2 DISCUSSION OF STABILITY UNDER FLUX CONDITIONS

As before in the case of flux conditions, the solution of the system (4.9) can be obtained as follows

$$v_{1j}(x,y,t) = \sum_{m=0}^{\infty} \sum_{n=0}^{\infty} \left[C_{mn} F_{mnj}(x)\ r \cosh(st)\ \exp(-\lambda_{mn}^{2} t) \right.$$

$$\left. + C'_{mn} F'_{mnj}(x) \sinh(st)\ \exp(-\lambda'^{2}_{mn} t) \right] \cos\left(\frac{n\pi y}{B}\right)$$

$$v_{2j}(x,y,t) = \sum_{m=0}^{\infty} \sum_{n=0}^{\infty} -\left[C_{mn} F_{mnj}(x) \sinh(st)\ \exp(-\lambda_{mn}^{2} t) \right.$$

$$\left. + C'_{mn} F'_{mnj}(x) \frac{\cosh(st)}{r} \exp(-\lambda'^{2}_{mn} t) \right] \cos\left(\frac{n\pi y}{B}\right) \quad (4.29)$$

where

$$C_{mn} = \frac{\int_0^L \int_0^B z_1(x,y,0) \cos\left(\frac{n\pi y}{B}\right) F_{mn}(x)\,dx\,dy}{\left|\left| F_{mn}(x) \cos\left(\frac{n\pi y}{B}\right) \right|\right|^2} \quad (4.30)$$

$$C'_{mn} = \frac{\int_0^L \int_0^B z_2(x,y,0) \cos\left(\frac{n\pi y}{B}\right) F'_{mn}(x)\,dx\,dy}{\left|\left| F'_{mn}(x) \cos\left(\frac{n\pi y}{B}\right) \right|\right|^2}$$

$$F_{mn1}(x) = \frac{\cos\left\{\frac{\lambda_{mn1} x}{\sqrt{D_{11x}}}\right\}}{\cos\left\{\frac{\lambda_{mn1} L_1}{\sqrt{D_{11x}}}\right\}} \quad (4.31)$$

$$F'_{mn1}(x) = \frac{\cos\left\{\frac{\lambda'_{mn1} x}{\sqrt{D_{21x}}}\right\}}{\cos\left\{\frac{\lambda'_{mn1} L_1}{\sqrt{D_{21x}}}\right\}}$$

and $F_{mnj}(x)$, $F'_{mnj}(x)$ are given by (4.17-b) and (4.18-b) respectively.

As before, using zero flux boundary conditions at the other end $x=L$, the equations determining λ_{mn}, λ'_{mn} can be obtained as

$$\frac{D_{1(N-1)x}}{D_{1Nx}} - \frac{\lambda_{mnN}\, F_{mn(N-1)}(L_{N-1})}{\sqrt{D_{1Nx}}\, \frac{d}{dx}\left[F_{mn(N-1)}(x)\right]_{x=L_{N-1}}} \cdot \tan\left[\frac{\lambda_{mnN}(L-L_{N-1})}{\sqrt{D_{1Nx}}}\right] = 0 \tag{4.32-a}$$

$$\frac{D_{2(N-1)x}}{D_{2Nx}} - \frac{\lambda'_{mnN}\, F'_{mn(N-1)}(L_{N-1})}{\sqrt{D_{2Nx}}\, \frac{d}{dx}\left[F'_{mn(N-1)}(x)\right]_{x=L_{N-1}}} \cdot \tan\left[\frac{\lambda'_{mnN}(L-L_{N-1})}{\sqrt{D_{2Nx}}}\right] = 0 \tag{4.32-b}$$

respectively.

From the solution (4.29) it can again be noted here that the stability condition in this case is also given by (4.25) where in this case λ_{11}, λ'_{11} are the minimum roots of (4.31-a) and (4.32-b) respectively which could even be zero as they would give nontrivial solution in (4.29). Thus, when $\lambda_{11} = \lambda'_{11} = 0$; the condition (4.25) will never be satisfied and hence the equilibrium state which is unstable without dispersion remains so with dispersion in patchy habitat under flux boundary conditions.

4.3.3 DISCUSSION OF STABILITY UNDER MIXED CONDITIONS

Proceeding in the same manner as before, the solution of the system (4.9) under mixed boundary conditions of type (4.5c) is given by

$$v_{1j}(x,y,t) = \sum_{m=1}^{\infty}\sum_{n=0}^{\infty} \Big[C_{mn}F_{mnj}(x)\ r\cosh(st)\exp(-\lambda_{mn}^{2}t) + C'_{mn}F'_{mnj}(x)\sinh(st)\exp(-\lambda'^{2}_{mn}t)\Big]\cos\left(\frac{n\pi y}{B}\right)$$

$$v_{2j}(x,y,t) = \sum_{m=1}^{\infty}\sum_{n=1}^{\infty} -\Big[C_{mn}F_{mnj}(x)\sinh(st)\exp(-\lambda_{mn}^{2}t) + C'_{mn}F'_{mnj}(x)\frac{\cosh(st)}{r}\exp(-\lambda'^{2}_{mn}t)\Big]\cos\left(\frac{n\pi y}{B}\right) \tag{4.33}$$

where C_{mn}, C'_{mn} are given by (4.20) and F_{mnj}, F'_{mnj} are given by (4.17), (4.18) respectively. Also λ_{mn}, λ'_{mn} in this case are the roots of equations (4.21). From the solution (4.33) it is obvious that the stability condition in this case also is given by (4.25) where λ_{11}, λ'_{11}, the minimum values of λ_{mn}, λ'_{mn}, correspond to m=1, n=0, [see(4.19)]. As discussed before λ_{11}, λ'_{11} remain nonzero in this case and would not depend upon the component of dispersion coefficients of the two species in y direction. As these minimum roots increases with dispersion of the species in x direction enhancing the degree of stability of the equilibrium state.

However, in the case of mixed boundary conditions of the type (4.5d), the solution can be obtained as

$$v_{1j}(x,y,t) = \sum_{m=0}^{\infty}\sum_{n=1}^{\infty} \Big[C_{mn}F_{mnj}(x)\ r\cosh(st)\exp(-\lambda_{mn}^{2}t) + C'_{mn}F'_{mnj}(x)\sinh(st)\exp(-\lambda'^{2}_{mn}t)\Big]\sin\left(\frac{n\pi y}{B}\right) \tag{4.34}$$

$$v_{2j}(x,y,t) = \sum_{m=0}^{\infty}\sum_{n=1}^{\infty} -\Big[C_{mn}F_{mnj}(x)\sinh(st)\exp(-\lambda_{mn}^{2}t) + C'_{mn}F'_{mnj}(x)\frac{\cosh(st)}{r}\exp(-\lambda'^{2}_{mn}t)\Big]\sin\left(\frac{n\pi y}{B}\right)$$

where C_{mn}, C'_{mn} are the same as (4.30), F_{mn1}, F'_{mn1} are given by (4.31) and F_{mnj}, F'_{mnj} by (4.17b), (4.18-b) respectively. In this case λ_{mnj}, λ'_{mnj} are the roots of equation (4.32) which could be zero also. Thus the minimum values of λ_{mn}, λ'_{mn} i.e. λ_{11}, λ'_{11} will now correspond to $m=0$, $n=1$ and would not depend upon the dispersion coefficient in x direction [see (4.19)]. As the condition for stability in this case is also given by (4.25) it can be noted here that degree of stability of the equilibrium state increases with dispersion coefficient in y direction.

Comparing these two cases of mixed boundary conditions with the case of flux boundary conditions, it can be noted that dispersion in a two dimensional rectangular habitat with reservoir boundary conditions along two opposite sides of the

habitat can make the equilibrium state stable which is unstable with zero flux boundary conditions all around the boundary.

4.3.4 THE CASE OF ONE DIMENSIONAL HABITAT

In the case of one dimensional habitat the solution of the system (4.9) with reservoir conditions can be obtained as follows :

$$v_{1j} = \sum_{n=1}^{\infty} \left[B_n T_{nj}(x)\, r \cosh(st) \exp(-w_n^2 t) + B_n' T_{nj}'(x) \sinh(st) \exp(-w_n'^2 t) \right]$$

$$v_{2j} = \sum_{n=1}^{\infty} - \left[B_n T_{nj}(x) \sinh(st) \exp(-w_n^2 t) + B_n' T_{nj}'(x)/r \cosh(st) \exp(-w_n'^2 t) \right] \tag{4.35}$$

$$j = 1,2,\ldots N$$

where

$$T_{n1}(x) = \frac{\sin\left(\frac{w_n x}{\sqrt{D_{11x}}}\right)}{\sin\left(\frac{w_n L_1}{\sqrt{D_{11x}}}\right)} \tag{4.36-a}$$

$$T_{nj}(x) = \cos\left[\frac{w_n(x-L_{j-1})}{\sqrt{D_{1jx}}}\right] T_{n(j-1)}(L_{j-1}) + \frac{D_{1(j-1)x}}{\sqrt{D_{2jx}}\, w_n} \sin\left[\frac{w_n(x-L_{j-1})}{\sqrt{D_{1jx}}}\right] \frac{d}{dx}\left[T_{n(j-1)}(x)\right]_{x=L_{j-1}} \tag{4.36-b}$$

$$T'_{n1}(x) = \frac{\operatorname{Sin}\left[\frac{w'_n x}{\sqrt{D_{21x}}}\right]}{\sin\left[\frac{w'_n L_1}{\sqrt{D_{21x}}}\right]} \qquad (4.37\text{-a})$$

$$T'_{nj}(x) = \cos\left[\frac{w'_n(x-L_{j-1})}{\sqrt{D_{2jx}}}\right] T'_{n(j-1)}(L_{j-1}) \qquad (4.37\text{-b})$$

$$+ \frac{D_{2(j-1)x}}{\sqrt{D_{2jx}}\, w'_n} \sin\left[\frac{w_n(x-L_{j-1})}{\sqrt{D_{2jx}}}\right] \frac{d}{dx}\left[T'_{n(j-1)}(x)\right]_{x=L_{j-1}}$$

$$B_n = \frac{\int_o^L Z_i(x,0)\; T_n(x)\, dx}{||T_n||^2} \qquad (4.38\text{-a})$$

$$B'_n = \frac{\int_o^L Z_i(x,0)\; T'_n(x)\, dx}{||T'_n||^2} \qquad (4.38\text{-b})$$

w_n, w'_n can be determined from the following equation

$$\frac{D_{1(N-1)x}}{D_{1Nx}} + \frac{w_n\, T_{n(N-1)}\,(L_{N-1})}{\sqrt{D_{1Nx}}\;\frac{d}{dx}\left[T_{n(N-1)}(x)\right]_{x=L_{N-1}}} \cot\left[\frac{w_n(L-L_{N-1})}{\sqrt{D_{1Nx}}}\right] = 0 \qquad (4.39)$$

$$\frac{D_{2(N-1)x}}{D_{2Nx}} + \frac{w'_n\, T'_{n(N-1)}\,(L_{N-1})}{\sqrt{D_{1Nx}}\;\frac{d}{dx}\left[T_{n(N-1)}(x)\right]_{x=L_{N-1}}} \cot\left[\frac{w'_n(L-L_{N-1})}{\sqrt{D_{2Nx}}}\right] = 0$$

The condition for stability of the equilibrium state in the patchy habitat is obtained as

$$w_n^2 \; w_n'^2 - s^2 > 0 \tag{4.40}$$

As seen before, the minimum roots w_1, w_1' increase with dispersion showing the enhancement of the degree of stability of the equilibrium state in this case also.

Further, comparing λ_{11}, λ_{11}' with w_1, w_1' in view of (4.19) it can be noted that even if the condition (4.25) is satisfied, the condition (4.40) may not be satisfied. Hence an equilibrium state can be stable in a two dimensional patchy habitat even if it is unstable in one dimensional patchy habitat.

In case of flux boundary conditions the solution of the system (4.9) is obtained as (4.35) with

$$T_{n1}(x) = \frac{\cos\left[\dfrac{w_n x}{\sqrt{D_{11x}}}\right]}{\cos\left[\dfrac{w_n L_1}{\sqrt{D_{11x}}}\right]}$$

$$T_{n2}(x) = \frac{\cos\left[\dfrac{w_n' x}{\sqrt{D_{21x}}}\right]}{\cos\left[\dfrac{w_n' x}{\sqrt{D_{21x}}}\right]} \tag{4.41}$$

and $T_{nj}(x)$, $T'_{nj}(x)$; $j=2,\ldots N$ are the same as (4.36-b), (4.37-b) respectively. The equations determining w_n, w'_n can be obtained as

$$\frac{D_{1(N-1)x}}{D_{1Nx}} - \frac{w_n\, T_{n(N-1)}(L_{N-1})}{\sqrt{D_{1Nx}}\; \frac{d}{dx}\left[T_{n(N-1)}(x)\right]_{x=L_{N-1}}} \cdot \tan\left[\frac{w_n(L-L_{N-1})}{\sqrt{D_{1Nx}}}\right]=0$$

$$\frac{D_{2(N-1)x}}{D_{2Nx}} - \frac{w'_n\, T'_{n(N-1)}(L_{N-1})}{\sqrt{D_{2Nx}}\; \frac{d}{dx}\left[T'_{n(N-1)}(x)\right]_{x=L_{N-1}}} \cdot \tan\left[\frac{w_n(L-L_{N-1})}{\sqrt{D_{2Nx}}}\right]= 0 \tag{4.42}$$

which give zero minimum roots for the nontrivial solution (4.35). As the condition for stability is the same as (4.40) in this case also, it can be noted that the equilibrium state is unstable under flux boundary conditions.

Thus, it is concluded that the equilibrium state which is always unstable under flux boundary condition in one dimensional patchy habitat may become stable under mixed boundary conditions of type (4.5-d) in a two dimensional habitat.

4.4 PREY PREDATOR MODEL

In case of prey-predator model the interaction functions are prescribed as follows

$$\begin{aligned} f_{1j} &= u_{1j}(a_1 - c_1 u_{2j}) \\ f_{2j} &= u_{2j}(-a_2 + c_2 u_{1j}) \end{aligned} \tag{4.43}$$

The linearized system, in this case, corresponding to (4.2) can be obtained from (4.8) as

$$\begin{aligned}\frac{\partial v_{1j}}{\partial t} &= -f v_{2j} + D_{1jx}\frac{\partial^2 v_{1j}}{\partial x^2} + D_{1jy}\frac{\partial^2 v_{1j}}{\partial y^2}\\ \frac{\partial v_{2j}}{\partial t} &= g v_{1j} + D_{2jx}\frac{\partial^2 v_{2j}}{\partial x^2} + D_{2jy}\frac{\partial^2 v_{2j}}{\partial y^2}\end{aligned} \qquad (4.44)$$

Using the following transformation

$$\begin{bmatrix} v_{1j} \\ v_{2j} \end{bmatrix} = \begin{bmatrix} r\cos(st) & \sin(st) \\ \sin(st) & -1/r\cos(st) \end{bmatrix}\begin{bmatrix} z_{1j} \\ z_{2j} \end{bmatrix} \qquad (4.45)$$

to system (4.3) and solving under boundary conditions (4.5-a) we get

$$v_{1j}(x,y,t) = \sum_{m=1}^{\infty}\sum_{n=1}^{\infty}\Big[C_{mn}\, r\, F_{mnj}\cos(st)\exp(-\lambda_{mn}^2 t) + C'_{mn}F'_{mnj}\sin(st)\exp(-\lambda'^2_{mn}t)\Big]$$

$$v_{2j}(x,y,t) = \sum_{m=1}^{\infty}\sum_{n=1}^{\infty}\Big[C_{mn}F_{mnj}(x)\sin(st)\exp(-\lambda_{mn}^2 t) - C'_{mn}/r\, F'_{mnj}(x)\cos(st)\exp(-\lambda'^2_{mn}t)\Big]$$

$$\sin\left(\frac{n\pi y}{B}\right)$$

where F_{mnj}, F'_{mnj}, C_{mn}, C'_{mn}, are defined, as before, in (4.17)–(4.20) and λ_{mn}, λ'_{mn} can be obtained from (4.21).

Analysing as before, it can be noted from (4.46) that the equilibrium state which is stable otherwise remains so even with dispersive migration of the species.

Further, similar analysis can be carried out for the boundary conditions (9-b), (9-c), (9-d) from which it can be noted that the stability of the equilibrium state increases with dispersion coefficients involved with reservoir conditions but would not depend upon dispersion coefficients associated with flux boundary conditions.

4.5 CONCLUSIONS

In this chapter, the linear stability of competition and prey-predator models in two dimensional rectangular patchy habitat has been discussed and the following conclusions are drawn from the linear stability analysis.

i. In the case of competition model, the equilibrium state which is unstable otherwise may become stable with dispersion when reservoir conditions are prescribed on the boundary of the habitat and the increase in dispersion coefficients of the species enhances the degree of stability of the equilibrium state.

ii. The equilibrium state for this competition model remains unstable even with dispersion under flux boundary conditions.

iii. The dispersion in a habitat with reservoir conditions along any two opposite sides of the rectangular habitat can stabilize the equilibrium state for competition model which

is unstable with zero flux boundary conditions all along the boundary.

iv. The equilibrium state in a competition model which is stable in a two dimensional habitat may not be stable in a linear one-dimensional habitat.

v. For prey predator model, the equilibrium state which is otherwise neutrally stable becomes stable for all types of boundary conditions discussed here.

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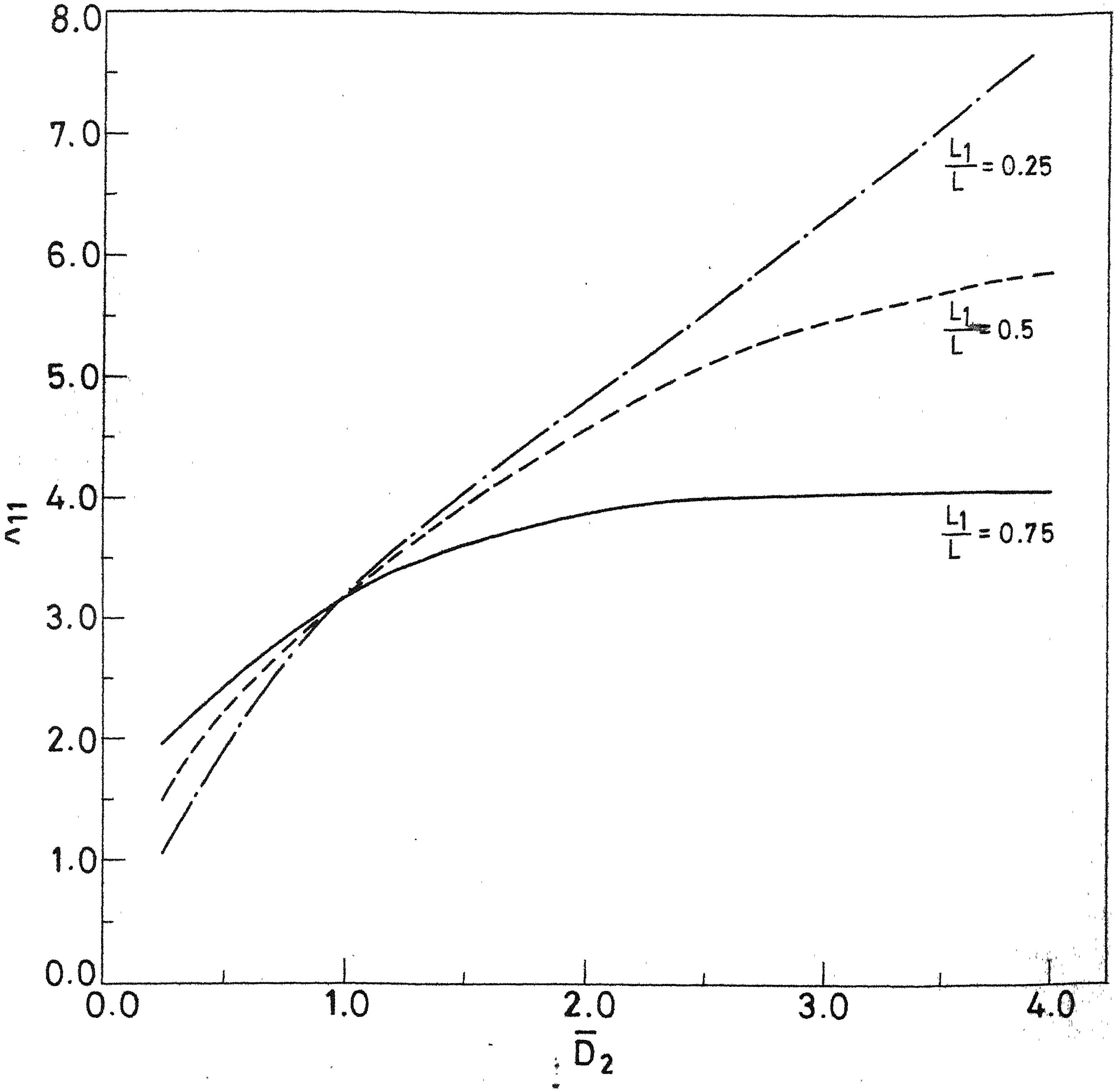

FIG. 1 VARIATION OF $\overline{\lambda}_{11}$ WITH $\overline{D}_2$

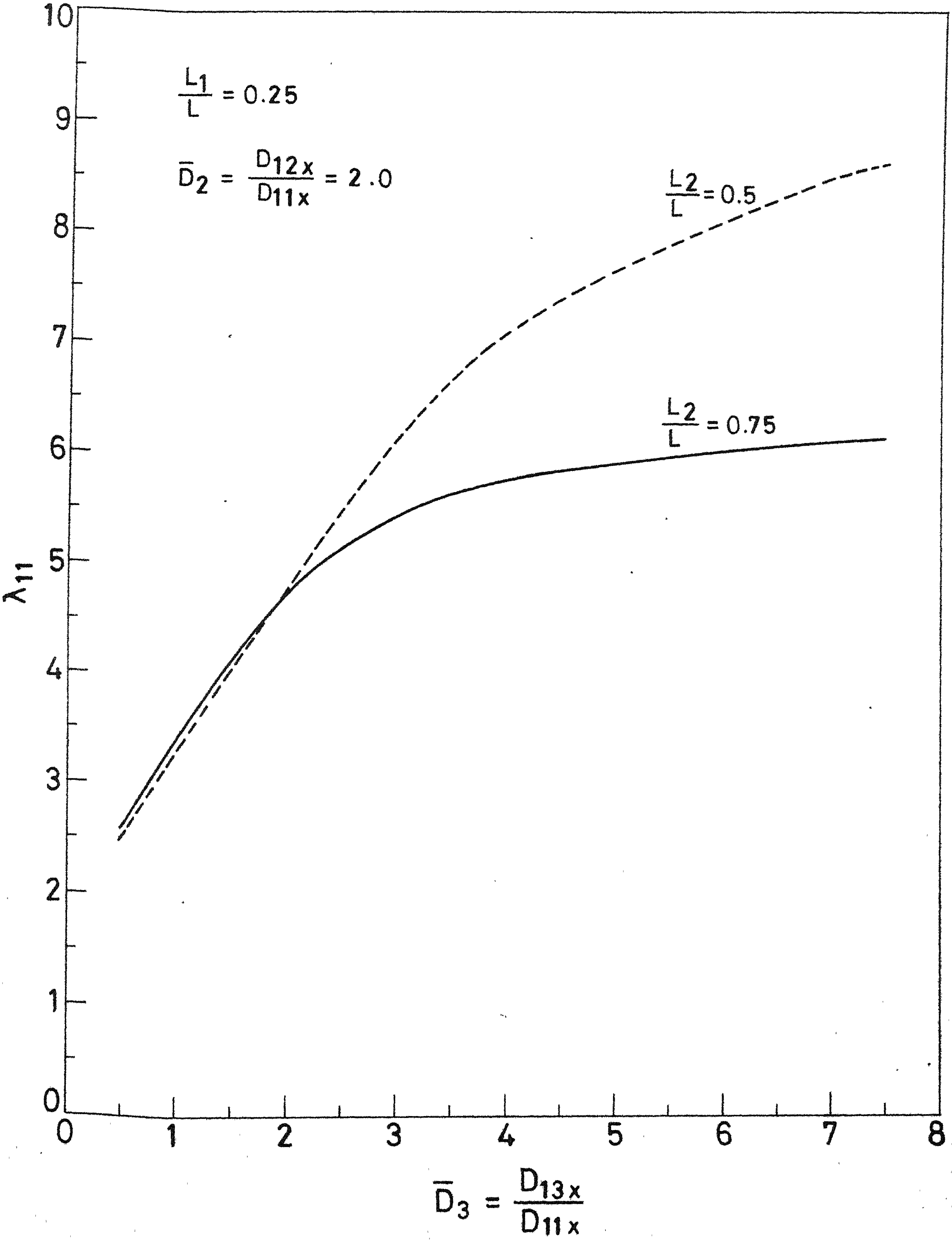

FIG. 2 VARIATION OF $\overline{\lambda}_{11}$ WITH $\overline{D}_3$

CHAPTER V

EFFECTS OF CONVECTIVE AND DISPERSIVE MIGRATION IN PATCHY HABITATS-I

5.1 INTRODUCTION

In Chapter IV, the effects of dispersive migrations on the linear stability of two interacting species system has been investigated in both one and two dimensional finite habitats and it has been shown that dispersion can stabilize an otherwise unstable equilibrium state.

It may be pointed out however, that the migration of the species can also be identified by convection which may arise due to biased dispersion (Comins and Blatt, 1974). The convective migration of the species can also arise because of sudden changes in ecological and environmental conditions in cases of heterogeneous habitats. It can be remarked that convective processes might play a dominant role over dispersive processes in affecting the evolution and coexistence of the species in a given habitat and thus the study of convective effects even in absence of dispersion may be of interest.

Keeping the above in view, in this chapter, the linear stability of two species system (Volterra type competition and prey predator models) in heterogeneous two dimensional habitats

consisting of finitely many connecting patches (sub-habitats) has been studied by taking into accounts the effects of convective migration in both longitudinal and transverse directions. The effects of dispersive migration in transverse direction has also been investigated.

Since it has been shown in Chapter II and III that the effects of species migration on linear stability of equilibrium state in cases of equal and unequal convection and dispersion are similar, in this chapter we therefore consider only the case of equal convection and dispersion for the two species wherever it is relevent.

5.2 BASIC EQUATIONS

Let us consider the evolution of two interacting and migrating species in a two dimensional $[0 < x, 0 < y < B]$ heterogeneous habitat divided into finitely many (say N) patches where jth patch $(j = 1,2,\ldots,N)$ is defined as $[L_{j-1} < x \leq L_j, 0 < y < B]$ with $L_0 = 0$. Then the evolution of two interacting and migrating species is governed by the following system of second order partial differential equations

$$\frac{\partial u_{ij}}{\partial t} + U_{ij}\frac{\partial u_{ij}}{\partial x} + V_{ij}\frac{\partial u_{ij}}{\partial y} = f_{ij} + D_{ijx}\frac{\partial^2 u_{ij}}{\partial x^2} + D_{ijy}\frac{\partial^2 u_{ij}}{\partial y^2}$$

$$i = 1,2,;\ j = 1,2,\ldots,N. \tag{5.1}$$

where f_{ij} corresponds to the usual Volterra term for the interaction of ith species in jth patch, U_{ij}, V_{ij} are the convective velocity components and (D_{ijx}, D_{ijy}) is the dispersion coefficient for the ith species in jth patch.

To simplify the analysis, it is assumed that the dispersive migration in the x direction is negligible in comparison to the dispersive migration in the y direction. This is feasible in the case of narrow habitat and when the convective velocities are dominant. It is further assumed that the migrative ability of the two species are same in respective patches. Keeping these in view, we have

$$\begin{aligned} D_{ijx} &\simeq 0 \quad ; \qquad i = 1,2 \\ D_{1jy} &= D_{2jy} = D_j \\ U_{1j} &= U_{2j} = U_j \qquad ; \ j = 1,2,\ldots,N \\ V_{1j} &= V_{2j} = V_j \end{aligned} \tag{5.2}$$

Assuming further that the nature of interaction of the two species are same in all the patches then the equilibrium state ($\bar{u}_{1j} = \bar{u}_1$, $u_{2j} = \bar{u}_2$) can be obtained by solving

$$f_{ij} = 0 \ ; \qquad i = 1,2;\ j = 1,2,\ldots,N.$$

Linearizing system (5.1) about the equilibrium point $(\bar{u}_1, \bar{u}_2)$ after making use of

$$u_{ij} = \bar{u}_i + v_{ij} \qquad i = 1,2 \tag{5.3}$$

in (5.1) we get

$$\frac{\partial v_{ij}}{\partial t} + U_j \frac{\partial v_{ij}}{\partial x} + V_j \frac{\partial v_{ij}}{\partial y} = \sum_{k=1}^{2} b_{ik} v_{kj} + D_j \frac{\partial^2 v_{ij}}{\partial y^2} \tag{5.4}$$

where $b_{ik} = \left(\frac{\partial f_i}{\partial u_k}\right)_{\bar{u}_1,\bar{u}_2}$; $i = 1,2$; $j = 1,2,\ldots,N$

where v_{ij}, $i,j = 1,2$ is the perturbation density of the ith species in the jth patch.

The system (5.4) is associated with the following initial, boundary and matching conditions :

$$v_{ij} = 0 \; ; \; i = 1,2 \; ; \quad j = 1,2,\ldots,N \text{ at } t = 0 \tag{5.5}$$

$$\left.\begin{aligned} v_{1j} &= N_j > 0 \quad j = 1,2,\ldots, N \text{ at } y = 0 \\ v_{2j} &= P_j > 0 \quad j = 1,2,\ldots,N \text{ at } y = 0 \end{aligned}\right. \tag{5.6}$$

$$v_{ij} = 0, \; y = B \quad \text{for } i = 1,2, \quad j = 1,2,\ldots,N \tag{5.7}$$

$$v_{i1} = 0, \text{ at } x = 0 \quad \text{for } i = 1,2 \tag{5.8}$$

$$v_{i,j-1} = v_{i,j} \text{ at } x = L_{j-1} \text{ for } i = 1,2 \qquad j = 2,3,\ldots,N-1. \tag{5.9}$$

The conditions (5.6) are the reservoir conditions prescribed at $y = 0$ and the conditions (5.9) are the matching conditions

prescribed at the interface of jth and (j-1)th patch, $j = 2, \ldots N$.

5.3 COMPETITION MODEL

Considering the case of Volterra type competition model, the interaction functions f_{1j}, f_{2j}; $j = 1,2$ are given by

$$
\begin{aligned}
f_{1j} &= u_{1j}\,(a_1 - c_1\, u_{2j}) \\
f_{2j} &= u_{2j}\,(a_2 - c_2\, u_{1j})
\end{aligned}
\qquad (5.10)
$$

which will give the positive equilibrium state as $(a_2/c_2, a_1/c_1)$. Using (5.10) the linearized system about the equilibrium state can be obtained as (5.4) with

$$
\begin{aligned}
b_{ii} &= 0 \\
b_{12} &= -f = -c_1 a_2/c_2 < 0 \\
b_{21} &= -g = -c_2 a_1/c_1 < 0
\end{aligned}
\qquad (5.11)
$$

5.3.1 FINITE HABITAT

For the finite habitat the solution of the system (5.4) with (5.11) in the first patch ($0 < x \leq L_1$, $0 < y < B$) after using the conditions (5.5) - (5.9) can be obtained as follows

$$v_{i1}(x,y,t) = \frac{2D_1\pi}{B^2} \sum_{m=1}^{\infty} mG_{i1}(t)\, \sin(m\pi y/B); \text{ for } t < x/U_1, \qquad (5.12)$$

$$v_{i1}(x,y,t) = \frac{2D_1\pi}{B^2} \sum_{m=1}^{\infty} m\bar{G}_{i1}(x)\, \sin(m\pi y/B); \text{ for } t > x/U_1, \qquad (5.13)$$

where

$$G_{ij}(a) = \int_0^a V_{ij}(T) \exp\left[\frac{V_j y}{2D_j} - F_j(m)\, T\right] dT$$

$$\bar{G}_{ij}(a) = 1/U_j \int_0^a V_{ij}(T/U_j) \exp\left[\frac{V_j y}{2D_j} - F_j(m)\, T/U_j\right] dT \qquad (5.14)$$

$$V_{1j}(T) = N_j \cosh(sT) - P_j r \sinh(sT)$$

$$(5.15)$$

$$V_{2j}(T) = P_j \cosh(sT) - N_j/r \sinh(sT)$$

$$F_j(m) = D_j m^2 \pi^2/B^2 + V_j^2/(4D_j) \qquad (5.16)$$

$$r = \sqrt{f/g}\ ,\ s = \sqrt{fg} \qquad (5.17)$$

Similarly in the jth patch ($L_{j-1} < x \leq L_j$; $0 < y < B$) solution of the system (5.4) with conditions (5.5) - (5.9) can be obtained as follows

$$v_{ij}(x,y,t) = 2D_j\pi/B^2 \sum_{m=1}^{\infty} mG_{ij}(t) \sin(m\pi y/B) \text{ for } t < \frac{x-L_{j-1}}{U_j}$$

$$(5.18)$$

$$v_{ij}(x,y,t) = J_{ij} + \bar{J}_{ij}\ ;\ i = 1,2;\quad \text{for } t > \frac{x-L_{j-1}}{U_j} \qquad (5.19)$$

where

$$J_{ij} = 2D_j\pi/B^2 \sum_{m=1}^{\infty} m\bar{G}_{ij}\left(\frac{x-L_{j-1}}{U_j}\right) \sin(m\pi y/B) \qquad (5.20)$$

$$\bar{J}_{ij} = 2/B \sum_{m=1}^{\infty} \exp\left[\frac{V_j y}{2D_j} - F_j(m)\frac{(x-L_{j-1})}{U_j}\right] K_{ij}(m) \sin\left(\frac{m\pi y}{B}\right)$$

$$(5.21)$$

$$K_{1j}(m) = \int_0^B \exp\left(-\frac{V_j}{2D_j}y\right)\Big[v_{1j-1}\left(L_{j-1},y,t-\frac{x-L_{j-1}}{U_j}\right)$$

$$\cosh\left\{s\left(\frac{x-L_{j-1}}{U_j}\right)\right\} - v_{2j-1}\left(L_{j-1},y,t-\frac{x-L_{j-1}}{U_j}\right) r$$

$$\sinh\left\{s\left(\frac{x-L_{j-1}}{U_j}\right)\right\}\Big] \sin(m\pi y/B)\, dy \qquad (5.22\text{-a})$$

$$K_{2j}(m) = \int_0^B \exp\left(-\frac{V_j}{2D_j}y\right)\Big[v_{2j}\left(L_{j-1},y,t-\frac{x-L_{j-1}}{U_j}\right).$$

$$\cosh\left\{s\left(\frac{x-L_{j-1}}{U_j}\right)\right\} - v_{1j-1}\left(L_{j-1},y,t-\frac{x-L_{j-1}}{U_j}\right)/r$$

$$\sinh\left\{s\left(\frac{x-L_{j-1}}{U_j}\right)\right\}\Big] \sin(m\pi y/B)\, dy \qquad (5.22\text{-b})$$

It is noticed from (5.12) and (5.13) that the population densities of the two species in the first patch remain unaffected by the presence of second patch for all times. However, it is clear from (5.18), (5.19) that population distributions in the second patch are dependent on the densities in the first patch for $t > \frac{x-L_1}{U_2}$ and may increase because of them. It is also noted here that for, $U_2 = 0$, even the second patch becomes isolated for $t > 0$.

5.3.2 DISCUSSION OF STABILITY IN TWO PATCHES

For simplicity, we first discuss the stability of the equilibrium state in the case when the habitat is consisting of only two patches, i.e. $N = 2$.

To see the asymptotic stability and the coexistence of two species around the equilibrium state, we investigate the behaviour of $v_{i1}(x,y,t)$ and $v_{i2}(x,y,t)$ for $i = 1,2$ as $t \to \infty$.

The linear stability of the equilibrium state in the first patch is discussed in the following cases :

Case 1 : Considering the case when there is no longitudinal (x-direction) convection in the first patch i.e. $U_1 = 0$, it can be noted from (5.12) that as $t \to \infty$, v_{11}, v_{21} tend to v^s_{11}, v^s_{21} respectively, (Gradshteyn, 1965) where

$$v^s_{11}(x,y) = 2D_1\pi/B^2 \exp\left(\frac{V_1}{2D_1}y\right)\sum_{m=1}^{\infty} m/\bar{D}_1(m)\left[F_1(m)N_1 - fP_1\right]\sin\frac{m\pi y}{B}) \tag{5.23}$$

$$v^s_{21}(x,y) = 2D_1\pi/B^2 \exp\left(\frac{V_1}{2D_1}y\right)\sum_{m=1}^{\infty} m/\bar{D}_1(m)\left[F_1(m)P_1 - gN_1\right]\sin\frac{m\pi y}{B})$$

$$\text{provided} \quad \pi^2 D_1/B^2 + V_1^2/(4D_1) - s > 0 \tag{5.24}$$

$$\text{where} \quad \bar{D}_j(m) = F_j^2(m) - s^2 \quad \text{for } j = 1 \tag{5.25}$$

It may be noted that (5.23) satisfies the steady state form of the system (5.4) with the corresponding boundary conditions, showing the asymptotic stability of the equilibrium state under the condition (5.24). It can be seen from (5.24) that stability increases (convergence is faster) as the transverse (y direction) convective velocity increases. Also in the absence of transverse convection the stability of equilibrium state increases with dispersal.

Further it can be seen from (5.12) that even if the condition (5.24) is not satisfied, the finite limit of $v_{i1}, i=1,2$ can be obtained under the condition

$$N_1 = P_1 r \tag{5.26}$$

as follows

$$v^s_{11}(x,y) = \frac{2D_1\pi}{B^2} \exp\left(\frac{V_1}{2D_1} y\right) \sum_{m=1}^{\infty} \frac{mN_1}{\bar{D}_{11}(m)} \cdot \sin(m\pi y/B)$$

$$v^s_{21}(x,y) = \frac{2D_1\pi}{B^2} \exp\left(\frac{V_1}{2D_1} y\right) \sum_{m=1}^{\infty} \frac{mP_1}{\bar{D}_{11}(m)} \cdot \sin(m\pi y/B) \tag{5.27}$$

where $\quad \bar{D}_{1j}(m) = m^2\pi^2 D_j/B^2 + V_j^2/(4D_j) + s, \; j = 1 \qquad (5.28)$

which is the same as the steady state solution of (5.4) with the corresponding boundary conditions showing the asymptotic stability of equilibrium state under the condition (5.26). If both the conditions are not satisfied the equilibrium state is unstable.

Case 2 : In the case when longitudinal convection is nonzero i.e. $U_1 \neq 0$, the density distributions of the two species as $t \to \infty$ are same as (5.13) which is also the steady state solution of the system (5.4) showing that the equilibrium state is always asymptotically stable. It can therefore be concluded here that the equilibrium state which is otherwise unstable is always stable with longitudinal convection in the absence of dispersion.

In the second patch also we have the following two possibilities.

Case 1 : When $U_2 = 0$, it has already been noted that the second patch is isolated and so the conditions for stability in this patch are obtained (as discussed in the first patch) as follows

$$\pi^2 D_j/B^2 + V_j^2/(4D_j) - s > 0 \tag{5.29}$$

or
$$N_j = P_j r \tag{5.30}$$
for $j = 2$.

It can be noted here that the condition for stability (5.24) or (5.26) and (5.29) or (5.30) in the two patches for $U_1 = 0$, and $U_2 = 0$ respectively are the same as can be obtained for one dimensional (y direction) homogeneous habitat.

Case 2 : For $U_2 \neq 0$ the population distribution v_{i2}, $i = 1,2$ is given by (5.18) and as $t \to \infty$ reduces to

$$v_{i2} = J_{i2} + \bar{J}_i \tag{5.31}$$

where J_{i2}, $i = 1,2$ is given in (6.20) which is always finite and $\bar{J}_i$ for $U_1 = 0$ is given by

$$\begin{aligned}\bar{J}_1 = 4D_1\pi/B^3 \sum_{m=1}^{\infty}\sum_{n=1}^{\infty} \exp\left[\frac{V_2}{2D_2}\, y - F_2(m)\left(\frac{x-L_1}{U_2}\right)\right] n/\bar{D}_2(n) \\ \left[F_1(n)V_{11}\left(\frac{x-L_1}{U_2}\right) - fV_{21}\left(\frac{x-L_1}{U_2}\right)\right] \theta(m,n)\sin(m\pi y/B)\end{aligned}$$

$$\tag{5.32}$$

$$\begin{aligned}\bar{J}_2 = 4D_1\pi/B^3 \sum_{m=1}^{\infty}\sum_{n=1}^{\infty} \exp\left[\frac{V_2}{2D_2}\, y - F_2(m)\left(\frac{x-L_1}{U_2}\right)\right] n/\bar{D}_2(n) \\ \left[F_1(n)V_{21}\left(\frac{x-L_1}{U_2}\right) - g\, V_{11}\left(\frac{x-L_1}{U_2}\right)\right] \theta(m,n)\sin(m\pi y/B)\end{aligned}$$

provided (5.24) is satisfied and

$$\bar{J}_1 = 4D_1\pi/B^3 \sum_{m=1}^{\infty} \sum_{n=1}^{\infty} \exp\left[\frac{V_2}{2D_2} y - F_2(m)\left(\frac{x-L_1}{U_2}\right)\right] n/\bar{D}_{11}(n) V_{11}\left(\frac{x-L_1}{U_2}\right)$$

$$\theta(m,n) \sin (m\pi y/B) \qquad (5.33)$$

$$\bar{J}_2 = 4D_1\pi/B^2 \sum_{m=1}^{\infty} \sum_{n=1}^{\infty} \exp\left[\frac{V_2}{2D_2} y - F_2(m)\left(\frac{x-L_1}{U_2}\right)\right] n/\bar{D}_{11}(n) V_{21}\left(\frac{x-L_1}{U_2}\right)$$

$$\theta(m,n) \sin (m\pi y/B)$$

provided (5.26) is valid. The constant $\theta(m,n)$ is given by

$$\theta(m,n) = A/2 \Big[\{ A^2 + (\tfrac{m-n}{B})^2 \pi^2 \}^{-1} \{\exp (AB)(-1)^{m-n} - 1 \} \qquad (5.34)$$

$$- \{ A^2 + (\tfrac{m+n}{B})^2 \pi^2 \}^{-1} \{\exp (AB)(-1)^{m+n} - 1 \} \Big]$$

where

$$A = \frac{V_1}{2D_1} - \frac{V_2}{2D_2}$$

and $V_{i1}(T)$, $F_j(n)$ are defined in (5.15), (5.16) respectively. It is noticed that (5.31) is the steady state solution of the system (5.4) with corresponding boundary conditions provided (5.24) or (5.26) is satisfied indicating the asymptotic stability of the equilibrium state under respective conditions. It is noted here that the condition for stability of the equilibrium state in the second patch is same as in the first patch showing that the equilibrium state in the second patch is stable provided it is stable in the first patch. However if none of the conditions (5.24) and (5.26) is satisfied, the equilibrium state

is unstable in both the patches and this situation arises due to zero longitudinal convective velocity in the first patch and nonzero in the second patch.

It is seen that when $U_1 \neq 0$ the expression for $\bar{J}_i$, i = 1,2 is obtained as follows

$$\bar{J}_i = 4D_1\pi/(U_1B^3) \sum_{m=1}^{\infty} \sum_{n=1}^{\infty} \exp\left[-F_2(m)\left(\frac{x-L_1}{U_2}\right) + \frac{V_2}{2D_2} y\right]$$

$$n\,\bar{K}_i(n)\,\theta(m,n)\,\sin(m\pi y/B) \qquad (5.35)$$

$$\text{where } \bar{K}_i(n) = \int_0^{L_1} \exp\{-F_1(n)T\}\,V_{i1}\left(\frac{x-L_1}{U_2} + T/U_1\right) dT \qquad (5.36)$$

It can again be noted that (5.31) with (5.35) is the steady state solution of the system (5.4) showing that the equilibrium state is always stable if the longitudinal convective velocities in the two patches remain nonzero. In particular, if the conditions throughout the habitat are identical, the equilibrium state is always stable in presence of longitudinal convection.

It may be concluded from the above that the patchiness may cause the instability of otherwise stable equilibrium state provided longitudinal convective velocity is zero in the first patch and nonzero in the second patch.

5.3.3 SEMI-INFINITE HABITAT

In the case of semi-infinite habitat (in y direction) the solution of the system (5.4) with (5.10) in the first patch

after using the conditions (5.5) - (5.9) can be obtained as follows

$$v_{i1}(x,y,t) = \int_0^t V_{i1}(T)\ \phi_1(x,y,T)dT \quad \text{for } t < x/U_1 \qquad (5.37)$$

$$v_{i1}(x,y,t) = \int_0^x V_{i1}\left(\frac{z}{U_1}\right)\psi_1(x,y,z)dz \quad \text{for } t > x/U_1 \qquad (5.38)$$

where $$\phi_j(x,y,T) = \frac{y}{2\sqrt{\pi D_j}}\ T^{-3/2}\exp\left[-(4D_jT)^{-1}(y-V_jT)^2\right] \qquad (5.39)$$

$$\psi_j(x,y,T) = \frac{y}{2\sqrt{\pi D_j/U_j}}\ Z^{-3/2}\exp\left[-(4D_jT/U_j)^{-1}(y-V_jT/U_j)^2\right]$$

$$(j = 1) \qquad (5.40)$$

and V_{i1}, $i = 1,2$ is defined in (5.15) for $j = 1$.

Similarly in the second patch, the distribution of species can be obtained by solving (5.4) with (5.10) and using conditions (5.7) - (5.9) as follows

$$v_{i2}(x,y,t) = \int_0^t V_{i2}(T)\ \phi_2(x,y,T)dT, \ \text{for } t < \frac{x-L_1}{U_2} \qquad (5.41)$$

$$v_{i2}(x,y,t) = E_i + E_i^! \ , \quad \text{for } t > \frac{x-L_1}{U_2} \qquad (5.42)$$

$$E_i = \int_0^{\bar{x}} V_{i2}(Z/U_2)\ \psi_2(x,y,z)\ dz \qquad (5.43)$$

$$E_i^! = \int_0^{\infty} \bar{\theta}(\bar{y},\bar{x})\ M_i(\bar{y})\ dy \qquad (5.44)$$

where

$$M_i(\bar{y}) = \int_0^{\bar{t}} V_{i1}(T+\bar{x}/V_2)\ \bar{\phi}_1(L_1,\bar{y},T)\ dT \qquad (5.45)$$

$$\bar{\phi}_1(L_1,\bar{y},T) = \phi_1(x,y,T) \quad \{1-H(T-L_1/U_1)\} \tag{5.46}$$

$$\bar{\theta}(\bar{y},\bar{x}) = \sqrt{\frac{U_2}{4\pi D_2\bar{x}}} \exp\left[-\frac{V_2^2\bar{x}}{4D_2U_2}\right] \tag{5.47}$$

$$\left[\exp\left\{-\frac{(y-\bar{y})^2U_2}{4D_2\bar{x}}\right\} - \exp\left\{-\frac{(y+\bar{y})^2U_2}{4D_2\bar{x}}\right\}\right] \tag{5.48}$$

$$\bar{x} = x-L_1, \; \bar{t} = t-\bar{x}/U_2.$$

and H is a unit step function.

It is clear from (5.37), (5.38) that the distribution of the species in the first patch are independent of the presence of second patch, while distribution in the second patch are dependent on the first patch for $t > \frac{x-L_1}{U_2}$. However, for $U_2 = 0$, even the second patch becomes isolated.

5.3.4 DISCUSSION OF STABILITY IN TWO PATCHES

In the first patch, when $U_1 = 0$, it can be seen that the finite limit of (5.37) as $t \to \infty$ would exist provided the condition (5.26) is satisfied and is given by,

$$\begin{aligned} v_{11} &= N_1 \exp\left[\frac{V_1}{2D_1}y - \left(\frac{V_1^2}{4D_1^2} + \frac{s}{D_1}\right)^{1/2} y\right] \\ v_{21} &= P_1 \exp\left[\frac{V_1}{2D_1}y - \left(\frac{V_1^2}{4D_1^2} + \frac{s}{D_1}\right)^{1/2} y\right] \end{aligned} \tag{5.49}$$

It can be verified that the condition (5.26) is also the necessary and sufficient condition for the existence of steady

state solution given by (5.49) showing the asymptotic stability of equilibrium state in the first patch.

For $U_1 \neq 0$, the solution v_{i1}, $i = 1,2$ tends to (5.38) as $t \to \infty$ which is the same as the steady state solution. Thus, it is concluded that with longitudinal convection the equilibrium state is always stable.

In the second patch for $U_2 = 0$, since this patch is isolated, similar results as discussed in the first patch are obtained here also and the condition for stability is (5.30).

When $U_2 \neq 0$ the limiting population densities as $t \to \infty$ can be obtained as follows :

$$v_{i2}(x,y) = E_i + \bar{E}_i \ , \quad i = 1,2 \tag{5.50}$$

where E_i is the same as defined earlier in (5.43) and $\bar{E}_i$ is given as follows :

$$\bar{E}_i = \int_0^\infty \bar{\theta}(\bar{y},\bar{x}) \bar{M}_i(\bar{y}) \, d\bar{y}, \quad i = 1,2 \tag{5.51}$$

where

$$\begin{aligned}\bar{M}_1(\bar{y}) &= N_1 \exp \{ \frac{V_1}{2D_1} \bar{y} - \frac{s\bar{x}}{U_2} - (\frac{V_1^2}{4D_1} + s)^{1/2} \bar{y}/\sqrt{D_1} \}. \\ \bar{M}_2(\bar{y}) &= P_1 \ \exp \{ \frac{V_1}{2D_1} \bar{y} - \frac{s\bar{x}}{U_2} - (\frac{V_1^2}{4D_1} + s)^{1/2} \bar{y}/\sqrt{D_1} \}\end{aligned} \tag{5.52}$$

for $U_1 = 0$, provided (5.26) is satisfied and

$$\bar{M}_i(\bar{y}) = \int_0^{L_1} V_{i1}(z/U_1 + \bar{x}/U_2) \ \psi_1(\bar{x},\bar{y},z)dz, \ i = 1,2 \tag{5.53}$$

for $U_1 \neq 0$.

Thus, it is concluded that for nonzero longitudinal convection in the second patch, the equilibrium state is always stable provided longitudinal convection is nonzero in the first patch. However, if it is zero in the first patch, the possibility of instability may arise because (5.26) may not be satisfied.

It can be remarked here that the convection and dispersion of the two species has no effect on the linear stability of the equilibrium state in case of semi infinite habitat. Therefore, in the following, we discuss the general case of N patches in finite habitat only.

5.4 STABILITY IN 'N' PATCHES

The stability of equilibrium state in the jth patch, $j = 2,\ldots,N$ is now discussed in the following two cases.

Case 1 : $U_j = 0$

For zero longitudinal convection in jth patch, it can be noted from (5.18) that this patch is isolated from all other patches. When $t \to \infty$ the limiting populations in this case are given by (5.23) or (5.27) for $j = 2,\ldots,N$ under condition (5.29) or (5.30) respectively which are also the steady state solution of the corresponding system, showing the asymptotic stability of equilibrium state in the jth patch.

Case 2 : $U_j \neq 0$.

When longitudinal convective velocity is nonzero, it can be seen from (5.19) that the densities of the two species in

jth patch depends upon the density distribution of the species in all the preceeding patches provided $U_k \neq 0$ for all k, such that $1 \leq k \leq j-1$. Thus the stability in this patch is dependent upon the stability of the equilibrium state in all the preceeding patches.

It can be seen that by solving the steady state system corresponding to (5.4) with (5.10) and using boundary conditions (5.5) - (5.9), the solution $v^s_{ij}(x,y)$, $i = 1,2$, $j = 2,3,\ldots,N$ is given as (5.19) - (5.22) when $v_{ij}(x,y,t)$ is replaced by $v^s_{ij}(x,y)$ in (5.19), $v_{ij-1}(L_{j-1},y,t - \frac{x-L_{j-1}}{U_j})$ by $v^s_{ij-1}(L_{j-1},y)$ in (5.22) for $j = 2,3,\ldots,N$ and $v_{i1}(L_{j-1}, y, t)$ by $v^s_{i1}(L_{j-1},y)$ in (5.13) for $i = 1,2$. It may be noted from (5.19) - (5.22) that the just mentioned steady state solution i.e. $v^s_{ij}(x,y)$, $i = 1,2$, $j = 2,3,\ldots,N$ is also the limit of $v_{ij}(x,y,t)$ as $t \to \infty$, showing that the equilibrium state is always asymptotically stable in all the patches $j = 2,3,\ldots,N$ with nonzero longitudinal convective velocity. In particular, it may be pointed out that if the conditions in all the patches become identical the equilibrium state would always be stable due to longitudinal convective migration of the species.

Further, it may happen that the longitudinal convective velocity is zero in atleast one patch preceeding to jth patch, say $U_k = 0$, $k < j$, such that $U_\ell \neq 0$ for $k < \ell < j$. As pointed out earlier the kth patch would become isolated from all other patches and the density distribution of the species in this patch

would be given by (5.18) for $j = k$ and the equilibrium state would be stable provided (5.29) or (5.30) is satisfied for $j = k$. However, if none of the conditions (5.29) and (5.30) is satisfied the equilibrium state in kth patch could be unstable.

It may be noted that in the jth patch, the distribution of species would depend upon the density distribution of species in all the patches preceeding to it till the kth patch, and would be given by (5.19) to (5.22) where $v_{ik}(x,y,t)$ is given by (5.18) for $j = k$, $i = 1,2$. Thus, the equilibrium state in jth patch would be stable (unstable) if it is stable (unstable) in the kth patch and the condition for stability (instability) in the jth patch remains the same as in the kth patch.

From the above discussions it may be noted that patchiness in a habitat caused by longitudinal convective migration may lead to instability of otherwise stable equilibrium state in this habitat.

5.5 PREY PREDATOR MODEL

In this case the interaction functions can be written as

$$f_{1j} = (a_1 - c_1 u_{2j}) u_{1j}$$
$$\qquad (5.54)$$
$$f_{2j} = (-a_2 + c_2 u_{1j}) u_{2j}$$

Using (5.54) the linearized system could be given by (5.4) with

$$b_{ii} = 0, \ i = 1,2$$

$$b_{12} = -f = -c_1 a_2/c_2 < 0 \tag{5.55}$$

$$b_{21} = g = c_2 a_1/c_1 > 0$$

Solving (5.4) with (5.54) and using conditions (5.5) - (5.9) the solution can be obtained as (5.12) - (5.22) where

$$V_{1j}(T) = N_j \cos(sT) - P_j r \sin(sT) \tag{5.56}$$

$$V_{2j}(T) = P_j \cos(sT) + N_j/r \sin(sT)$$

It can be noted that from the solution with (5.55) that the first patch is always isolated but the density distribution of species on the jth patch $j = 2,3,\ldots,N$ are very much dependent on all the preceeding patches for $U_k \neq 0$, $k < j$ but it is independent of all the succeeding patches. It can be seen here that in this case the equilibrium state which is stable otherwise is always stable with patchiness also.

5.6 CONCLUSIONS

In this chapter effects of patchiness on the linear stability of two interacting and migrating species have been discussed by assuming that the interaction coefficients are not affected by the patchiness of the habitat.

In the case of competition model in the habitat with two patches only it has been shown that for nonzero longitudinal convection and zero longitudinal dispersion in both the patches the equilibrium state is always stable with or without transverse convection and dispersion in finite or infinite habitats. The first patch is always isolated but for zero longitudinal convection even the second patch becomes isolated and the conditions for stability of the equilibrium state have been obtained as (5.24) or (5.26) and (5.29) or (5.30) in the two patches in the case of finite habitat. It can be noted from (5.24) and (5.29) that the stability of equilibrium state increases with transverse convection. However, if the transverse convection is absent the stability increases due to species dispersal. But in case of infinite habitat the transverse convection and dispersion have no effect on stability and the conditions for stability are (5.26) and (5.30) in respective patches. These results are same as would have been obtained in the case of one dimensional habitats.

For nonzero longitudinal convection in the second patch, it is noted that the equilibrium state in this patch is stable provided it is stable in the first patch. In particular, when longitudinal convection is zero in the first patch, then the equilibrium state may become unstable in both the patches, indicating that the patchiness may have destabilizing effect in both the finite and infinite habitats.

For the habitats with N patches it has been shown that in absence of longitudinal convection in the jth patch the condition for stability of the equilibrium state is similar to as obtained in the first patch. However if the longitudinal convective velocity is nonzero in the jth patch then the stability (instability) in this patch depends upon the stability (instability) of equilibrium state in all previous patches. In particular, if longitudinal convective velocity is nonzero in all the patches preceeding to jth patch then the equilibrium state is always stable in this patch.

In case of prey predator model, it has been shown that the equilibrium state which is stable otherwise, remain stable with patchiness also.

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CHAPTER VI

EFFECTS OF CONVECTIVE AND DISPERSIVE MIGRATION IN PATCHY HABITATS

6.1 INTRODUCTION

In Chapter V, effects of convection on linear stability of two interacting and migrating species system in two dimensional habitats consisting of finitely many patches have been investigated by considering both transverse and longitudinal convection in all the patches and dispersion only in the transverse direction (i.e. parallel to the interfaces of the patches). However the effect of longitudinal dispersion has not been considered.

Keeping this in view, in this chapter, we study the linear stability of two interacting and migrating species system by considering various combinations of convection and dispersion in patchy habitats.

6.2 BASIC EQUATIONS

Consider the evolution of two interacting and migrating species in a patchy habitat consisting of two or finitely many patches. By taking into account the convection and dispersion, the governing system for the evolution of two species in the jth patch can be given by equation (3.4) in Chapter III.

Assuming the interaction coefficients of the species to be unaffected by the patchiness of the habitat, the nontrivial

uniform positive equilibrium state ($\bar{u}_{ij} = \bar{u}_i$, $i = 1,2; j=1,2,\ldots,N$) of the system (3.4) can be obtained by solving

$$f_{ij} = 0 \; ; \; i = 1,2; \; j = 1,2,\ldots,N$$

Linearization of the governing system (3.4) would give

$$\frac{\partial u_{ij}}{dt} + U_{ij} \frac{\partial v_{ij}}{\partial x} + V_{ij} \frac{\partial v_{ij}}{\partial y} = \sum_{k=1}^{2} b_{ik} v_{kj} + D_{ijx} \frac{\partial^2 v_{ij}}{\partial x} + D_{ijy} \frac{\partial^2 v_{ij}}{\partial y^2} \tag{6.1}$$

To study the linear stability of the equilibrium state the system (6.1) is solved in one and two dimensional habitats under suitable initial and boundary conditions which would be specified in particular cases studied.

It may be noted here that this coupled linear system (6.1) cannot be solved in a patchy habitat due to involvement of matching conditions at the interfaces of the patches and hence the following particular cases, involving some combinations of dispersive and convective migration of the species are studied.

(i) One dimensional patchy habitat consisting of two or N-patches with species having dispersion only in the last patch while convection in all the patches.

(ii) Two-dimensional patchy habitat consisting of two patches with species having longitudinal dispersion in the second patch, while transverse dispersion in both the patches.

(iii) Two-dimensional patchy habitat consisting of two patches with species having transverse dispersions different in the two patches.

6.3 EFFECTS OF MIGRATION IN A ONE DIMENSIONAL HABITAT : TWO PATCHES

Consider the habitat $0 < x \leq L$ to be divided into two linear patches by a line $x = L_1$ such that first patch is defined as $0 < x \leq L_1$ and second patch as $L_1 < x \leq L_2$.

It is assumed that the second patch is ecologically more favourable to both the species and hence the tendency of convective migration of the species in the first patch is more and dispersive migration may be negligible i.e. $D_{i1} = 0$, $i = 1,2$. But in the second patch both convection and dispersive migration are dominant. It is also assumed that the convective velocities for the species are same in the respective patches i.e. $U_{1j} = U_{2j} = U_j$, $j = 1,2$ while the dispersal coefficients are same $(D_{12} = D_{22} = D)$ in the second patch.

With these assumptions, the system (6.1) may be linearized about the equilibrium state by writing

$$u_{ij}(x,t) = \bar{u}_i + v_{ij}(x,t), \quad i,\ j = 1,2$$

to get

$$\frac{\partial v_{ij}}{\partial t} + U_j \frac{\partial v_{ij}}{\partial x} = \sum_{k=1}^{2} b_{ik}\, v_{kj} \ ;$$

$$j = 1,\ 0 < x \leq L \qquad (6.2\text{-a})$$

$$\frac{\partial v_{ij}}{\partial t} + U_j \frac{\partial v_{ij}}{\partial x} = \sum_{k=1}^{2} b_{2k} v_{kj} + D \frac{\partial^2 v_{ij}}{\partial x^2}; \; j = 2, L_1 < x < L \tag{6.2-b}$$

where

$$b_{ik} = \left(\frac{\partial f_i}{\partial u_k}\right)_{\bar{u}_1, \bar{u}_2} .$$

The system (6.2) may be associated with the following initial and boundary conditions

$$v_{ij}(x,0) = 0; \quad i,j = 1,2, \quad x > 0 \tag{6.3}$$

$$\left.\begin{array}{l} v_{11}(0,t) = \bar{N}_1 > 0 \\ v_{21}(0,t) = \bar{P}_1 > 0, \end{array}\right\} \; t > 0 \tag{6.4}$$

$$\left.\begin{array}{l} v_{12}(x,t) \to 0, \\ v_{22}(x,t) \to 0, \end{array}\right\} \; t > 0 \tag{6.5}$$

as $x \to \infty$ for semi-infinite habitat or as $x \to L$, for finite habitat.

The condition (6.4) implies that there exists a reservoir for both the species at $x = 0$. At the interface $x = L_1$ of the two interconnecting patches, the following matching conditions are prescribed :

$$\underset{x \to L_1}{\mathrm{Lt}} \; v_{12}(x,t) = v_{11}(L_1,t)$$

$$\underset{x \to L_1}{\mathrm{Lt}} \; v_{22}(x,t) = v_{21}(L_1,t) \tag{6.6}$$

6.3.1 COMPETITION MODEL

In the case of competition model, the interaction functions are given by,

$$f_{1j} = u_{1j}(a_1 - c_1\, u_{2j})$$

$$f_{2j} = u_{2j}(a_2 - c_2 u_{1j}) \tag{6.7}$$

where u_{1j} and u_{2j}; $j = 1,2$, denote the densities of two species in jth patch. The corresponding linearized system for the evolution of the two species are given by (6.2) with

$$b_{ii} = 0\ , \qquad i = 1,2,$$

$$b_{12} = -f = -\, c_1 a_2/c_2 < 0 \tag{6.8}$$

$$f, g > 0$$

$$b_{21} = -g = -\, c_2 a_1/c_1 < 0$$

(i) Semi-infinite habitat

Solving system (6.2-a) with (6.8) and using conditions (6.3) and (6.4), the distribution of the species in the first patch are obtained as follows :

$$v_{11} = V_{11}\ (\frac{x}{U_1})\ H(t - \frac{x}{U_1})$$

$$v_{21} = V_{21}\ (\frac{x}{U_1})\ H(t - \frac{x}{U_1}) \tag{6.9}$$

where

$$V_{11}(t) = \bar{N}_1 \cosh st - \bar{P}_1 r \sinh st$$

$$V_{21}(t) = \bar{P}_1 \cosh st - \frac{\bar{N}_1}{r} \sinh st \tag{6.10}$$

$$s = \sqrt{b_{12} \cdot b_{21}} \quad , \; r = \sqrt{b_{12}/b_{22}} \tag{6.11}$$

and $H(t - \frac{x}{U_1})$ is the unit step function.

Similarly, solving the system (6.2-b) with conditions (6.3), (6.4), (6.6) corresponding to infinite habitat, the distributions of the species in the second patch by using the transformation similar to (6.8), are obtained as

$$v_{12} = \int_0^t \phi_2(x-L_1, t-T) V_{11}(t-T+\frac{L_1}{U_1})\, H(T - \frac{L_1}{U_1})\, dT$$

$$v_{22} = \int_0^t \phi_2(x-L_1, t-T) V_{21}(t-T+\frac{L_1}{U_1})\, H(T - \frac{L_1}{U_1})\, dT \tag{6.12}$$

where

$$\phi_j(x,t) = \frac{1}{t^{3/2}} \cdot \frac{x}{2\sqrt{\pi D}} \exp\left(- \frac{(x - U_j t)^2}{4Dt}\right) \tag{6.13}$$

and $j = 2$.

It may be noted from equation (6.9) and (6.12) that for $U_1 = 0$, no species exists in any patch as expected from initial and boundary conditions. From (6.9) it can be seen that, at any instant $t = \frac{x_1}{U_1}$, $U_1 \neq 0$ the species in the region $0 < x < x_1$ have nonuniform spatial distributions while in the

region $x > x_1$ the densities are zero. It may also be noted that the distribution of species in the first patch are unaffected by the presence of second patch. However, it can be seen from (6.12) that the populations in the second patch are very much dependent on the size of the first patch and the conditions prescribed at the boundary of the first patch.

As $t \to \infty$ it can be seen from (6.9) and (6.10) that the limits of $v_{11}(x,t)$ and $v_{21}(x,t)$ approach to $V_{11}(x/U_1)$ and $V_{21}(x/U_1)$ respectively which are the steady state solutions of the system (6.2-a) showing that the equilibrium state is always asymptotically stable.

From (6.12) it is noticed that as $t \to \infty$ the populations v_{12}, v_{22} would respectively tend to

$$
\left.
\begin{aligned}
v^s_{12}(x) &= V_{11}\left(\frac{L_1}{U_1}\right) \exp\left[\frac{U_2}{2D}(x-L_1) - \left(\frac{U_2^2}{4D} + s\right)^{1/2} \left(\frac{x-L_1}{\sqrt{D}}\right)\right] \\
v^s_{22}(x) &= V_{21}\left(\frac{L_1}{U_1}\right) \exp\left[\frac{U_2}{2D}(x-L_1) - \left(\frac{U_2^2}{4D} + s\right)^{1/2} \left(\frac{x-L_1}{\sqrt{D}}\right)\right]
\end{aligned}
\right\} \quad (6.14)
$$

provided

$$\bar{N}_1 = \bar{P}_1 \, r \qquad (6.15)$$

It can be verified that (6.14) is the steady state solution of the system (6.2-b) which would exist under (6.15) showing that the equilibrium state is asymptotically stable in the second patch also, but the convective and dispersive migration have no effect on stability. It is also noted here

that the stability condition (6.15) depends upon the boundary conditions prescribed at the first patch.

Considering the particular case as $L_1 \to 0$ i.e. the single patch $0 < x < \infty$ the equilibrium is asymptotically stable provided condition (6.15) is satisfied which is the same as obtained by Gopalsamy (1977).

When, $L_1 \to \infty$, the habitat reduces to a single patch again and the equilibrium state is stable and the steady state distributions of the species are given by (6.9) showing non-uniform spatial patterns arising due to convective migration.

(ii) Finite habitat

In the case of finite habitat of length L, the solution in the first patch remains the same as obtained in (6.9) and the equilibrium state remains stable. However, in the second patch ($L_1 < x < L$) the solution of the system (6.2-b), with initial condition (6.3) boundary condition (6.5) at $x = L$ and the matching condition (6.6), by using the transformation (6.14) is obtained as follows

$$v_{12}(x,t) = \frac{2D\pi}{(L-L_1)^2} \sum_{m=1}^{\infty} m\, G_{11}(L_1) \sin\left[\frac{m\pi(x-L_1)}{L-L_1}\right]$$
$$v_{22}(x,t) = \frac{2D\pi}{(L-L_1)^2} = \sum_{m=1}^{\infty} m\, G_{21}(L_1) \sin\left[\frac{m\pi(x-L_1)}{L-L_1}\right] \qquad (6.16)$$

where,

$$G_{11}(L_1) = \int_0^t F_2(t-T,x-L_1)V_{11}(t-T+\frac{L_1}{U_1})\ H(T-\frac{L_1}{U_1})\ dT$$

$$G_{21}(L_1) = \int_0^t F_2(t-T,x-L_1)V_{21}(t-T+\frac{L_1}{U_1})\ H(T-\frac{L_1}{U_1})\ dT \tag{6.17}$$

$$F_j(t,x) = \exp\left[-\frac{Dm^2\pi^2 t}{(L-L_{j-1})^2} - \frac{U_j^2\, t}{4D} + \frac{U_j\, x}{2D}\right], \tag{6.18}$$

and $j = 2$.

It is noticed from (6.16) and (6.18) that as $t \to \infty$, $v_{12}(x,t)$, $v_{22}(x,t)$ tend to

$$v_{12}(x) = \frac{2D\pi}{(L-L_1)^2} \sum_{m=1}^{\infty} m\ \bar{G}_{11}(L_1)\ \sin\left(\frac{m\pi(x-L_1)}{L-L_1}\right)$$

$$v_{22}(x) = \frac{2D\pi}{(L-L_1)^2} \sum_{m=1}^{\infty} m\ \bar{G}_{21}(L_1)\ \sin\left(\frac{m\pi(x-L_1)}{(L-L_1)}\right) \tag{6.19}$$

where

$$\bar{G}_{11}(L_1) = \exp\left[\frac{U_2}{2D}(x-L_1)\right]\cdot\left[V_{11}(\frac{L_1}{U_1})(\frac{Dm^2\pi^2}{(L-L_1)^2} + \frac{U_2^2}{4D}) - f\ V_{21}(\frac{L_1}{U_1})\right]/\bar{D}_2$$

$$\bar{G}_{21}(L_1) = \exp\left[\frac{U_2}{2D}(x-L_1)\right]\cdot\left[V_{21}(\frac{L_1}{U_1})(\frac{Dm^2\pi^2}{(L-L_1)^2} + \frac{U_2^2}{4D}) - gV_{11}(\frac{L_1}{U_1})\right]/\bar{D}_2 \tag{6.20}$$

$$\bar{D}_j = (\frac{m^2\pi^2 D}{(L-L_{j-1})^2} + \frac{U_j^2}{4D})^2 - s^2 \tag{6.21}$$

provided

$$\frac{Dm^2\pi^2}{(L-L_1)^2} + \frac{U_2^2}{4D} - s > 0 \tag{6.22}$$

It may be seen that these distributions are the steady state solution of the system (6.2-b) with conditions (6.5), (6.6) showing that the equilibrium state is asymptotically stable under the condition (6.22) and the stability increases as convective velocity or the length of first patch increases. It may also be seen from (6.22) that if convection is absent, the stability increases as dispersal coefficient increases.

It may be noted again that even if the condition (6.22) is not satisfied, the limit of $v_{12}(x,t)$ and $v_{22}(x,t)$ can exist provided condition (6.15) is valid, giving

$$v_{12}(x) = \frac{2D\pi}{(L-L_1)^2} \exp\left(\frac{U_2}{2D}(x-L_1)\right) \sum_{m=1}^{\infty} \frac{m}{\bar{D}_{21}} V_{11}\left(\frac{L_1}{U_1}\right) \sin\left[\frac{m\pi(x-L_1)}{(L-L_1)}\right]$$

$$v_{22}(x) = \frac{2D\pi}{(L-L_1)^2} \exp\left(\frac{U_2}{2D}(x-L_1)\right) \sum_{m=1}^{\infty} \frac{m}{\bar{D}_{21}} V_{21}\left(\frac{L_1}{U_1}\right) \sin\left[\frac{m\pi(x-L_1)}{L-L_1}\right] \tag{6.23}$$

where

$$\bar{D}_{j1} = \frac{m^2\pi^2 D}{(L-L_{j-1})^2} + \frac{U_j^2}{4D} + s, \quad j = 2 \tag{6.24}$$

which also satisfy the steady state system corresponding to (6.2-b) with boundary conditions (6.5) - (6.6) showing again the asymptotic stability of the equilibrium state under the condition (6.15), however, the stability does not depend upon convective and dispersive migration.

6.3.2 PREY PREDATOR MODEL

Considering the case of Volterra type prey predator system the interaction functions may be written as

$$f_{1j} = u_{1j}\,(a_1 - c_1\, u_{2j})$$

$$f_{2j} = u_{2j}(-a_2 + c_2\, u_{1j})\ ;\ j = 1,2 \qquad (6.25)$$

where u_{1j} and u_{2j} denote the densities of prey and predators in the jth patch. Then the equations governing the evolution are given by (6.2) with

$$b_{ii} = 0$$

$$b_{12} = -f \qquad f,g > 0 \qquad (6.26)$$

$$b_{21} = g$$

(i) SEMI-INFINITE HABITAT

The solution of the system (6.2) with (6.26) under conditions (6.3) - (6.6) in respective patches are given by (6.9) and (6.12) where $V_{11}(t)$, $V_{21}(t)$ are modified as follows :

$$V_{11}(t) = V_{12}(t) = N_1 \cos(st) - P_1 r \sin(st)$$

$$V_{21}(t) = V_{22}(t) = \frac{N_1}{r} \sin(st) + P_1 \cos(st) \qquad (6.27)$$

In this case also as $t \to \infty$ the population distributions in the first patch tend to nonuniform spatial steady state

distributions showing that the equilibrium state is asymptotically stable.

In the second patch the limiting populations of two species as $t \to \infty$ can be obtained from (6.12) and (6.27) as follows

$$v_{12}(x) = \exp\left[-k_1(x-L_1)\right] V_{12}\left[k_2(x-L_1) + \frac{s L_1}{U_1}\right]$$

$$v_{22}(x) = \exp\left[-k_1(x-L_1)\right] V_{22}\left[k_2(x-L_1) + \frac{s L_1}{U_1}\right] \tag{6.28}$$

where

$$k_1 = \left[\frac{U_2^2}{8D^2} + \frac{1}{2D}\left(\frac{U_2^4}{16D^2} + s^2\right)^{1/2}\right]^{1/2} - \frac{U_2}{2D}$$

$$k_2 = \left[-\frac{U_2^2}{8D^2} + \frac{1}{2D}\left(\frac{U_2^4}{16D^2} + s^2\right)^{1/2}\right]^{1/2} \tag{6.29}$$

As the distributions (6.28) are also the steady state solution of the system (6.2-b) with (6.26), the equilibrium is asymptotically stable.

Since $(x-L_1)$ decreases as L_1 increases therefore v_{12}, v_{22} increases as L_1 increases. Thus, it may be noted from equation (6.28) that larger the patch 1, higher the densities of preys and predators in the second patch.

For the case $L_1 = 0$, $U_2 = 0$ the distributions (6.28) are the same as obtained by Hadelar (1974).

(ii) FINITE HABITAT

Consider the prey predator model given by (6.26) in the case of finite habitat. The solutions in the first patch remains the same as (6.9) with (6.27) while in the second patch the distribution of the species can be obtained as

$$v_{12}(x,t) = \frac{2D\pi}{(L-L_1)^2} \sum_{m=1}^{\infty} m\, G_{12}(L_1) \sin\left[\frac{m\pi(x-L_1)}{L-L_1}\right]$$

$$v_{22}(x,t) = \frac{2D\pi}{(L-L_1)^2} \sum_{m=1}^{\infty} m\, G_{22}(L_1) \sin\left[\frac{m\pi(x-L_1)}{L-L_1}\right] \tag{6.30}$$

where

$$G_{12}(L_1) = \int_0^t F_2(t-T,x-L_1).V_{12}(t-T+\frac{L_1}{U_1})\, u(T-\frac{L_1}{U_1})dT$$

$$G_{22}(L_1) = \int_0^t F_2(t-T,x-L_1).V_{22}(t-T+\frac{L_1}{U_1})\, u(T-\frac{L_1}{U_1})dT \tag{6.31}$$

and $F_2(t,x)$ is the same as in (6.18).

As discussed before, the equilibrium state is always asymptotically stable in the first patch.

In the second patch the distributions in the limiting case as $t \to \infty$ can be obtained from (6.30) by noting from (6.18) that the coefficient of t is always negative,

$$v_{12}(x) = \frac{2D\pi}{(L-L_1)^2} \sum_{m=1}^{\infty} m \; \bar{G}_{12}(L_1) \sin\left(\frac{m\pi(x-L_1)}{L-L_1}\right)$$

(6.32)

$$v_{22}(x) = \frac{2D\pi}{(L-L_1)^2} \sum_{m=1}^{\infty} m \; \bar{G}_{22}(L_1) \sin\left(\frac{m\pi(x-L_1)}{L-L_1}\right)$$

where

$$\bar{G}_{12}(L_1) = \exp\left[\frac{U_2}{2D}(x-L_1)\right] \cdot \left[V_{12}\left(\frac{L_1}{U_1}\right) \cdot \left(\frac{Dm^2\pi^2}{(L-L_1)^2} + \frac{U_2^2}{4D}\right) - f \; V_{22}\left(\frac{L_1}{U_1}\right)\right] / \bar{D}_2 ,$$

(6.33)

$$\bar{G}_{22}(L_1) = \exp\left[\frac{U_2}{2D}(x-L_1)\right] \cdot \left[g \; V_{12}\left(\frac{L_1}{U_1}\right) + \left(\frac{Dm^2\pi^2}{(L-L_1)^2} + \frac{U_2^2}{4D}\right) V_{22}\left(\frac{L_1}{U_1}\right)\right] / \bar{D}_2$$

which is the same as the steady state solution showing the asymptotic stability of the equilibrium state and the stability increases with convection.

6.3.3 EFFECTS OF MIGRATION IN FINITE NUMBER OF PATCHES

Let us consider that the habitat is divided into finitely many patches, say n. Then the linearized equations in this case are given by (6.2-a) where $i = 1,2$, $j = 1,2,\ldots,n$ and jth patch corresponds to $L_{j-1} < x \leq L_j$ with $L_o = 0$.

We discuss the following cases :

(i) When only convective migration is present in all patches.

(ii) When in the first (n-1) patches convective migration is present while in the last patch dispersive migration is also present.

In case (i) for competition model with interaction functions (6.8), the solution of equations (6.2-a) with conditions (6.3), (6.5) and the matching conditions at the interface $x = L_{j-1}$

$$v_{i,j-1}(L_{j-1}) = v_{i,j}(L_{j-1}) \quad i = 1,2,\ j = 2,\dots,n \tag{6.34}$$

can be obtained as

$$\left.\begin{aligned} v_{1j}(x,t) &= V_{11}(T_j(x))\,\bar{H}_j(t,x) \\ v_{2j}(x,t) &= V_{21}(T_j(x))\,\bar{H}_j(t,x) \end{aligned}\right\} \quad \begin{aligned} &j = 1,2,\dots,n \\ &L_{j-1} < x < L_j \end{aligned} \tag{6.35}$$

where

$$\begin{aligned} T_j(x) &= \frac{x - L_{j-1}}{U_j} \text{ for } j = 1 \\ & \qquad\qquad\qquad\qquad 1 < j < n \\ T_j(x) &= \frac{x - L_{j-1}}{U_j} + \sum_{k=1}^{j-1} \frac{L_k - L_{k-1}}{U_k} \end{aligned} \tag{6.36}$$

and

$$\begin{aligned} \bar{H}_j(t,x) &= H\left(t - \frac{x - L_{j-1}}{U_j}\right) \quad \text{for } j = 1 \\ &= H\left(t - \frac{x-L_{j-1}}{U_j}\right) \prod_{i=2}^{j} H\left(t - \frac{x-L_{j-1}}{U_j} - \sum_{k=2}^{i} \frac{L_{k-1}-L_{k-2}}{U_{k-1}}\right) \\ & \qquad\qquad\qquad\qquad j > 1. \end{aligned} \tag{6.37}$$

It can be seen from (6.35) that as $t \to \infty$ the limiting populations in the jth patch are

$$\begin{aligned} v_{1j}(x) &= V_{11}(T_j(x)) \\ v_{2j}(x) &= V_{21}(T_j(x)) \end{aligned} \tag{6.38}$$

which is the same as the steady state solutions of the corresponding system showing that the equilibrium state is asymptotically stable.

Considering the case (ii) for the competition model again the solution in the jth patch for $1 \leq j \leq n-1$ is the same as obtained in (6.35). In the nth patch of infinite extent the solution of (6.2-b) using interaction coefficients (6.8) with conditions (6.3), (6.5) and the matching condition,

$$v_{i,n-1}(L_{n-1}) = v_{in}(L_{n-1}) \tag{6.39}$$

is given by

$$v_{1n}(x) = \int_0^t \phi_n(x-L_{n-1}, t-T).V_{11}(t-T+T_{n-1}(L_{n-1}))\bar{H}_{n-1}(T,L_{n-1})\, dT$$

(6.40)

$$v_{2n}(x) = \int_0^t \phi_n(x-L_{n-1}, t-T).V_{21}(t-T+T_{n-1}(L_{n-1}))\bar{H}_{n-1}(T,L_{n-1})\, dT$$

where $\phi_n(x,t)$ is given by (6.13) when $j = n$ and $v_{1j}(t)$, $T_{n-1}(L_{n-1})$, $\bar{H}(T,L_{n-1})$ are given in (6.35) - (6.37) respectively. As $t \to \infty$, the population distribution in the nth patch can be obtained from (6.40) as follows :

$$v_{1n} = V_{11}(T_{n-1}(L_{n-1}))\, \exp\left[\frac{U_n}{2D}(x-L_{n-1})-\left(\frac{U_n^2}{4D} + s\right)^{1/2}\left(\frac{x-L_{n-1}}{\sqrt{D}}\right)\right]$$

(6.41)

$$v_{2n} = V_{21}(T_{n-1}(L_{n-1}))\, \exp\left[\frac{U_n}{2D}(x-L_{n-1})-\left(\frac{U_n^2}{4D} + s\right)^{1/2}\left(\frac{x-L_{n-1}}{\sqrt{D}}\right)\right]$$

provided (6.15) is satisfied.

It can be verified that the steady state solution of the system (6.2-b) with conditions (6.5), (6.39) will exist provided (6.15) is satisfied and it is the same as (6.41) showing the asymptotic stability of equilibrium state which does not depend upon convective and dispersive migration.

If the nth patch is finite then the distribution of species can be obtained from (6.2-b) and (6.8) as

$$v_{1n}(x,t) = \frac{2D\pi}{(L-L_{n-1})^2} \sum_{m=1}^{\infty} m \; J_{1n}(L_{n-1}) \sin\left[\frac{m\pi(x-L_{n-1})}{(L-L_{n-1})}\right]$$

$$v_{2n}(x,t) = \frac{2D\pi}{(L-L_{n-1})^2} \sum_{m=1}^{\infty} m \; J_{2n}(L_{n-1}) \sin\left[\frac{m\pi(x-L_{n-1})}{(L-L_{n-1})}\right] \tag{6.42}$$

where

$$J_{1n}(L_{n-1}) = \int_0^t F_n(t-T,x-L_{n-1})V_{11}(t-T+T_{n-1}(L_{n-1}))\bar{H}_{n-1}(T,L_{n-1})\,dT$$

$$J_{2n}(L_{n-1}) = \int_0^t F_n(t-T,x-L_{n-1})V_{21}(t-T+T_{n-1}(L_{n-1}))\bar{H}_{n-1}(T,L_{n-1})\,dT \tag{6.43}$$

$F_n(t,x)$ is given by (6.18) for $j = n$,

and $V_{i1}(T)$ and $\bar{H}_{n-1}(T,L_{n-1})$ are defined in (6.35) and (6.37) respectively.

As discussed before when $t \to \infty$ the finite limit of (6.42) would exist provided

$$\frac{D\,m^2\,\pi^2}{(L-L_{n-1})^2} + \frac{U_n^2}{4D} - s > 0 \tag{6.44}$$

or condition (6.15) is satisfied giving the steady state solutions in these cases respectively as follows

$$v_{1n}(x) = \frac{2D\pi}{(L-L_{n-1})^2} \sum_{m=1}^{\infty} m \ \bar{J}_{1n}(L_{n-1}) \sin\left[\frac{m\pi(x-L_{n-1})}{L-L_{n-1}}\right]$$

(6.45)

$$v_{2n}(x) = \frac{2D\pi}{(L-L_{n-1})^2} \sum_{m=1}^{\infty} m \ \bar{J}_{2n}(L_{n-1}) \sin\left(\frac{m\pi(x-L_{n-1})}{L-L_{n-1}}\right)$$

and

$$v_{1n}(x) = \frac{2D\pi}{(L-L_{n-1})^2} \exp\left[\frac{U_n}{2D}(x-L_{n-1})\right] \sum_{m=1}^{\infty} \frac{m}{\bar{D}_{n1}} V_{11}(T_{n-1}(L_{n-1})) \sin\left[\frac{m\pi(x-L_{n-1})}{(L-L_{n-1})}\right]$$

(6.46)

$$v_{2n}(x) = \frac{2D\pi}{(L-L_{n-1})^2} \exp\left[\frac{U_2}{2D}(x-L_{n-1})\right] \sum_{m=1}^{\infty} \frac{m}{\bar{D}_{n1}} V_{21}(T_{n-1}(L_{n-1})) \sin\left[\frac{m\pi(x-L_{n-1})}{(L-L_{n-1})}\right]$$

where

$$\bar{J}_{1n} = \exp \frac{U_2}{2D}\left[(x-L_{n-1})\right] \cdot \left[V_{11}(T_{n-1}(L_{n-1}))\left(\frac{Dm^2\pi^2}{(L-L_{n-1})^2} + \frac{U_n^2}{4D}\right) - f\, V_{21}(T_{n-1}(L_{n-1}))\right] / \bar{D}_n$$

$$\bar{J}_{2n}(L_{n-1}) = \exp\left[\frac{U_n}{2D}(x-L_{n-1})\right] \cdot \left[V_{21}(T_{n-1}(L_{n-1}))\left(\frac{Dm^2\pi^2}{(L-L_{n-1})^2} + \frac{U_n^2}{4D}\right) - g\, V_{11}(T_{n-1}(L_{n-1}))\right] / \bar{D}_n \qquad (6.47)$$

$\bar{D}_n$ and $\bar{D}_{n1}$ are given by (6.21), (6.24) respectively when $j = n$ which shows that the equilibrium state is asymptotically stable under the condition (6.44) or (6.15). In particular from (6.44) it is noted that stability increases as convective velocity or the length of first n-1 patches increases. Further in absence of convection, stability increases with dispersion.

Finally, it can be remarked here that Case (i) is a one dimensional version of the problem studied in Chapter IV. However, Case (ii) may be regarded as a particular case of two subhabitats with first patch having variable convection approximating as (n-1) step functions while the second patch with constant convection and dispersion.

6.4 EFFECTS OF MIGRATION IN TWO DIMENSIONAL PATCHY HABITAT : TWO PATCHES

Consider the following particular cases of two competing species in a two dimensional heterogeneous habitat consisting of only two patches when

1. Convective velocity of both the species in the two patches are equal, i.e.

$$U_{ij} = U_j \qquad i = 1,2; \; j = 1,2$$
$$V_{ij} = V_j$$

2. Longitudinal dispersion in first patch is zero for both the species i.e.

$$D_{i1x} = 0, \quad i = 1,2 \,.$$

3. Dispersion for both the species are equal in two patches i.e.

$$D_{i2x} = D_1 \quad , \quad D_{i2y} = D_2$$

$$D_{i1y} = D$$

Under these assumptions the governing linearized system (6.1) for competing species can be written as

$$\frac{\partial v_{i1}}{\partial t} + U_1 \frac{\partial v_{i1}}{\partial x} + V_1 \frac{\partial v_{i1}}{\partial y} = \sum_{k=1}^{2} b_{ik} v_{k1} + D \frac{\partial^2 v_{i1}}{\partial y^2} \tag{6.48-a}$$

$$\frac{\partial v_{i2}}{\partial t} + U_2 \frac{\partial v_{i2}}{\partial x} + V_2 \frac{\partial v_{i2}}{\partial y} = \sum_{k=1}^{2} b_{ik} v_{k2} + D_1 \frac{\partial^2 v_{i2}}{\partial x^2} + D_2 \frac{\partial^2 v_{i2}}{\partial y^2} \tag{6.48-b}$$

with interaction functions (6.7).

The linearized system (6.48) is solved under following conditions

$$v_{ij}(x,y,0) = 0 \quad ; \quad i, j = 1,2 \tag{6.49}$$

$$v_{1j}(x,0,t) = N_j \quad ; \quad v_{2j}(x,0,t) = P_j \qquad j = 1,2 \tag{6.50}$$

$$v_{ij}(x,y,t) \to 0 \text{ as } y \to B \; ; \; i, j = 1,2 \tag{6.51}$$

$$\left.\begin{aligned} &v_{ij}(0,y,t) = 0 \; ; \; i = 1,2; \; j = 1 \\ &v_{ij}(x,y,t) \to 0 \text{ as } x \to L \quad , \quad i = 1,2 \; ; \; j = 2 \end{aligned}\right. \tag{6.52}$$

$$\operatorname*{Lt}_{x \to L_1} v_{i2}(x,y,t) = v_{i1}(L_1,y,t) \; ; \; i = 1,2 \tag{6.53}$$

Since in this case the situation in the first patch is same as discussed in Chapter V, the solution of (6.48-a) with conditions (6.49) - (6.52) are same as (5.18) - (5.22) and the condition for asymptotic stability in the first patch is given as

$$\frac{\pi^2 D}{B^2} + \frac{V_1^2}{4D} - s > 0$$

or

$$N_1 = P_1 r \ .$$

Again the solution of the system (6.48-b), (6.53) in the second patch can be obtained as,

$$v_{i2}(x,y,t) = J_{i2}(x,y,t) + \bar{J}_{i2}(x,y,t) \tag{6.56}$$

where

$$J_{i2} = \frac{4\pi D_2}{\bar{L}B^2} \sum_{m=1}^{\infty} \sum_{n=1}^{\infty} n \ . \ G_i^*(t,m,n)\ \theta(m)$$

$$\sin \frac{m\pi(x-L_1)}{\bar{L}} \sin \frac{n\pi y}{B} \tag{6.57}$$

$$\bar{J}_{i2} = \frac{4\pi D_1}{\bar{L}^2 B} \sum_{m=1}^{\infty} \sum_{n=1}^{\infty} m\ \bar{G}_i^*(t,m,n)$$

$$\sin \frac{m\pi(x-L_1)}{\bar{L}} \sin \frac{n\pi y}{B} \tag{6.58}$$

$$G_i^*(t,m,n) = \int_0^t V_{i2}(T) \exp\left[-\frac{U_2}{2D_1}(x-L_1) + \frac{V_2}{2D_2}\, y - F_2(m,n)T\right] dT$$

(6.59)

$$\bar{G}_i^*(t,m,n) = \frac{2\pi D}{B^2} \sum_{k=1}^{n} k\, I(k,n) \,.$$

$$\int_0^t \int_0^{t-T} V_{i1}(T+T_1)\exp\left[\frac{U_2}{2D_1}(x-L_1) + \frac{V_2}{2D_2}\,y - F_1(k)T_1 - F_2(m,n)T\right]$$

$$\left[1 - H(T_1 - \frac{L_1}{U_1}\right] dT_1 dT \tag{6.60}$$

$$F_1(k) = \frac{k^2\pi^2 D}{B^2} + \frac{V_1^2}{4D} \tag{6.61-a}$$

$$F_2(m,n) = \frac{m^2\pi^2 D_1}{\bar{L}^2} + \frac{n^2\pi^2 D_2}{B^2} + \frac{U_2^2}{4D_1} + \frac{V_2^2}{4D_2} \tag{6.61-b}$$

$$\theta(m) = \frac{m\pi}{\bar{L}}\left[1-(-1)^m \exp\left(-\frac{U_2 L_1}{2D_1}\right]\left[\frac{m^2\pi^2}{L^2} + \frac{U_2^2}{4D_1^2}\right]^{-1} \tag{6.62}$$

$$I(k,n) = \int_0^{\bar{L}} \exp\left[\left(\frac{V_1}{2D} - \frac{V_2}{2D_2}\right)y\right] \sin\frac{k\pi y}{B} \sin\frac{n\pi y}{B}\, dy \tag{6.63}$$

$$\bar{L} = L - L_1$$

and $H(t)$ is the unit step function.

In the second patch, it can be noted from (6.56) - (6.60) that the distribution of species is very much dependent upon the distribution of species in the first patch. As, $t \to \infty$, finite limits of v_{i2}, $i = 1,2$ would exist provided J_{i2} and $\bar{J}_{i2}$ are finite as $t \to \infty$. Let us explore the possibilities under which this may happen.

It can be seen from (6.57) that, as $t \to \infty$, the limits of J_{i2}, $i = 1,2$ exist, provided

$$\frac{\pi^2 D_1}{\bar{L}^2} + \frac{\pi^2 D_2}{B^2} + \frac{U_2^2}{4D_1} + \frac{V_2^2}{4D_2} - s > 0 \tag{6.64}$$

or
$$N_2 = P_2\, r \tag{6.65}$$

and would be given by

$$\underset{t \to \infty}{\mathrm{Lt}}\ J_{12} = \frac{4\pi D_2}{\bar{L}B^2} \exp\left[\frac{U_2}{2D_1}(x-L_1) + \frac{V_2}{2D_2} y\right] \cdot \sum_{m=1}^{\infty}\sum_{n=1}^{\infty} \frac{n\theta(m)}{\bar{F}_2(m,n)}\left[N_2F_2(m,n) - fP_2\right] \cdot \sin\frac{m\pi(x-L_1)}{\bar{L}} \cdot \sin\frac{n\pi y}{B} \tag{6.66-a}$$

$$\underset{t \to \infty}{\mathrm{Lt}}\ J_{22} = \frac{4\pi D_2}{\bar{L}B^2} \cdot \exp\left[\frac{U_2}{2D_1}(x-L_1) + \frac{V_2}{2D_2} y\right] \cdot \sum_{m=1}^{\infty}\sum_{n=1}^{\infty} \frac{n\theta(m)}{\bar{F}_2(m,n)}\left[P_2F_2(m,n) - gN_2\right] \cdot \sin\frac{m\pi(x-L_1)}{\bar{L}} \cdot \sin\frac{n\pi y}{B} \tag{6.66-b}$$

where

$$\bar{F}_2(m,n) = F_2^2(m,n) - s^2 \tag{6.67}$$

or

$$\underset{t \to \infty}{\mathrm{Lt}}\ J_{12} = \frac{4\pi D_2}{\bar{L}B^2} \cdot \exp\left[\frac{U_2}{2D_1}(x-L_1) + \frac{V_2}{2D_2} y\right] \cdot \sum_{m=1}^{\infty}\sum_{n=1}^{\infty} \frac{n\theta(m)N_2}{\bar{F}_{22}(m,n)} \sin\frac{m\pi(x-L_1)}{\bar{L}} \sin\frac{n\pi y}{B} \tag{6.68-a}$$

$$\underset{t \to \infty}{\mathrm{Lt}} \; J_{22} = \frac{4\pi D_2}{\bar{L}B^2} \cdot \exp\left[\frac{U_2}{2D_1}(x-L_1) + \frac{V_2}{2D_2}\,y\right] \cdot$$

$$\sum_{m=1}^{\infty}\sum_{n=1}^{\infty} \frac{n\theta(m)\,P_2}{\bar{F}_{22}(m,n)} \sin\frac{m\pi(x-L_1)}{\bar{L}} \sin\frac{n\pi y}{B} \qquad (6.68\text{-b})$$

where,

$$\bar{F}_{22}(m,n) = F_2(m,n) + s \qquad (6.69)$$

under conditions (6.64) or (6.65) respectively.

However, if longitudinal convective velocity is zero in the first patch then the finite limits of $\bar{J}_{i2}$ as $t \to \infty$ would exist provided

(i) (6.54) and (6.64) **are** satisfied, or

(ii) (6.55) is satisfied

and the corresponding limits are given by

$$\underset{t \to \infty}{\mathrm{Lt}} \; \bar{J}_{i2} = \frac{8\pi^2 DD_1}{\bar{L}^2 B^3} \cdot \exp\left[\frac{U_2}{2D_1}(x-L_1) + \frac{V_2}{2D_2}\,y\right] \cdot$$

$$\sum_{m=1}^{\infty}\sum_{n=1}^{\infty} \frac{m\,I_i(m,n)}{\bar{F}_2(m,n)} \sin\frac{m\pi(x-L_1)}{\bar{L}} \sin\frac{n\pi y}{B} \qquad (6.70\text{-a})$$

where

$$I_1(m,n) = \sum_{k=1}^{\infty} \frac{k\,I(k,n)}{\bar{F}_1(k)} \Big[F_1(k)\,\{N_1F_2(m,n) - f\,P_1\} \qquad (6.70\text{-b})$$

$$- f\,\{P_1F_2(m,n) - g\,N_1\}\Big]$$

$$I_2(m,n) = \sum_{k=1}^{\infty} \frac{k\, I(k,n)}{\bar{F}_1(k)} \Big[F_1(k) \;\{ P_1\, F_2(m,n) - g\, N_1 \} \tag{6.70-c}$$

$$- g\,\{ N_1\, F_2(m,n) - f\, P_1 \} \Big]$$

$$\bar{F}_1(k) = F_1^2(k) - s^2 \tag{6.70-d}$$

or

$$\underset{t \to \infty}{\mathrm{Lt}}\; \bar{J}_{12} = \frac{8\pi^2 DD_1}{\bar{L}^2 B^3} \exp \left[\frac{U_2(x-L_1)}{2D_1} + \frac{V_2}{2D_2}\, y \right] \tag{6.71-a}$$

$$\sum_{m=1}^{\infty} \sum_{n=1}^{\infty} \frac{m\, \bar{I}(n) N_1}{\bar{F}_{22}(m,n)} \sin \frac{m\pi(x-L_1)}{\bar{L}} \sin \frac{n\pi y}{B}$$

$$\underset{t \to \infty}{\mathrm{Lt}}\; \bar{J}_{22} = \frac{P_1}{N_1} \underset{t \to \infty}{\mathrm{Lt}}\; \bar{J}_{12} \tag{6.71-b}$$

$$\bar{I}(n) = \sum_{k=1}^{\infty} \frac{k\, I(k,n)}{F_1(k) + s} \tag{6.71-c}$$

When longitudinal convective velocity is nonzero in the first patch then the finite limit of $\bar{J}_{i2}$ as $t \to \infty$ would exist again provided (6.64) or (6.55) is satisfied and the limits can be obtained as follows :

$$\underset{t \to \infty}{\mathrm{Lt}}\; \bar{J}_{12} = \frac{8\pi^2 DD_1}{\bar{L}^2 B^3} \exp \left[\frac{U_2}{2D_1}(x-L_1) + \frac{V_1}{2D}\, y + \frac{V_2}{2D_2}\, y \right] \tag{6.72-a}$$

$$\sum_{m=1}^{\infty} \sum_{n=1}^{\infty} \frac{I_3(m,n)}{\bar{F}_2(m,n)} \cdot \sin \frac{m\pi(x-L_1)}{\bar{L}} \sin \frac{n\pi y}{B}$$

$$\underset{t \to \infty}{\mathrm{Lt}}\; \bar{J}_{22} = \frac{8\pi^2 DD_1}{L^2 B^3} \cdot \exp \left[\frac{U_2}{2D_1}(x-L_1) + \frac{V_1}{2D}\, y + \frac{V_2}{2D_2}\, y \right] \tag{6.72-b}$$

$$\sum_{m=1}^{\infty} \sum_{n=1}^{\infty} \frac{m\, I_4(m,n)}{\bar{F}_2(m,n)} \cdot \sin \frac{m\pi(x-L_1)}{\bar{L}} \cdot \sin \frac{n\pi y}{B}$$

$$I_3(m,n) = \sum_{k=1}^{\infty} k\, I(k,n) \left[F_2(m,n)\, \bar{G}_1(L_1,k) - f\, \bar{G}_2(L_1,k) \right] \qquad (6.72\text{-c})$$

$$I_4(m,n) = \sum_{k=1}^{\infty} k\, I(k,n) \left[F_2(m,n)\, \bar{G}_2(L_1,k) - g\, \bar{G}_1(L_1,k) \right] \qquad (6.72\text{-d})$$

$$\bar{G}_i(L_1,k) = \frac{1}{U_1} \int_0^x V_{i1}(Z/U_1) \exp\left[\frac{V_1}{2D}\, y - F_1(k)\, Z/U_1 \right] dZ \qquad (6.72\text{-e})$$

under (6.64) and

$$\underset{t \to \infty}{\mathrm{Lt}}\ \bar{J}_{12} = \frac{8\pi^2 D D_1}{\bar{L}^2 B^3} \left[1 - \exp\left(-\frac{L_1}{U_1}\right) \right] . \exp\left[\frac{U_2}{2D_1}(x-L_1) + \frac{V_2}{2D_2}\, y \right] \qquad (6.73\text{-a})$$

$$\sum_{m=1}^{\infty} \sum_{n=1}^{\infty} \frac{m\, \bar{I}(n)}{\bar{F}_{22}(m,n)}\, N_1 \sin \frac{m\pi(x-L_1)}{\bar{L}} \cdot \sin \frac{n\pi y}{B}$$

$$\underset{t \to \infty}{\mathrm{Lt}}\ \bar{J}_{22} = \frac{P_1}{N_1}\ \underset{t \to \infty}{\mathrm{Lt}}\ \bar{J}_{12} \qquad (6.73\text{-b})$$

when (6.55) is satisfied.

Keeping in view of finite limits of J_{i2} and $\bar{J}_{i2}$ under different conditions as pointed out above, it can be noted from (6.56) that finite limits of $v_{i2}(x,y,t)$ $i = 1,2$, as $t \to \infty$ would exist under one of the following alternatives, for $U_1 = 0$,

A1 : (6.54) and (6.64) are satisfied

A2 : (6.55) and (6.64) are satisfied

A3 : (6.55) and (6.65) are satisfied.

Similarly the finite limits of $v_{i2}(x,y,t)$ as $t \to \infty$ would exist under one of the following alternatives, for $U_1 \neq 0$,

A3 : (6.55) and (6.65) are satisfied

A4 : (6.64) is satisfied.

Now, it can be verified that under above alternatives A1 - A3 and A3, A4 the limiting population $v_{i2}(x,y,t)$ as $t \to \infty$ are the same as the steady state distributions $v^s_{i2}(x,y)$ of the corresponding system given by

$$v^s_{i2}(x,y) = \underset{t \to \infty}{Lt} J_{i2} + \underset{t \to \infty}{Lt} \bar{J}_{i2}$$

for $U_1 = 0$ and $U_1 \neq 0$ respectively, showing that the equilibrium state is stable in the second patch.

However, if none of these alternatives is satisfied, the equilibrium state in the second patch is unstable.

When longitudinal convective velocity is zero in the first patch and (6.54), (6.55) are not satisfied, it can be noted from A1 - A3 that the equilibrium state which is unstable in the first patch remains so in the second patch also. It is also seen that even when the equilibrium state is stable in the first patch, it may not be so in the second patch.

When $U_1 \neq 0$, the situation is fairly complex and whether the stability of the equilibrium state in the second patch depends on the first patch or not would be decided by the alternatives (A3 or A4) satisfied by the system. In particular, for $U_1 \neq 0$ the equilibrium state which is always stable in the first patch may remain so in the second patch also (see A4).

It is also noted that for sufficiently small and nonzero values of dispersion coefficients and nonzero convective migration the condition (6.54), (6.55) can always be made to satisfy and hence the equilibrium state is always stable in both the patches.

From the above discussion, it may be concluded that for competition model, the patchiness of the habitat may cause instability of the equilibrium state which may be stable otherwise.

6.5 EFFECTS OF PATCHINESS DUE TO TRANSVERSE DISPERSION IN A TWO DIMENSIONAL HABITAT : TWO PATCHES

In the following, another particular case of competing species in a two dimensional finite habitat is considered when

1. Transverse convection for the two species in both the patches is zero $V_{ij} = 0, \quad i,j = 1,2.$
2. Longitudinal convection and dispersion for the two species are equal in the two patches i.e.

$$U_{ij} = U \quad ; \; i,j = 1,2$$

$$D_{ijx} = D \quad ; \; i,j = 1,2$$

Under these assumptions, the governing linearized system for competing species can be written as

$$\frac{\partial v_{ij}}{\partial t} + U \frac{\partial v_{ij}}{\partial x} = \sum_{k=1}^{2} b_{ik} v_{ij} + D \frac{\partial^2 u_{ij}}{\partial x^2} + D_{ijy} \frac{\partial^2 u_{ij}}{\partial y^2}, \; i,j = 1,2 \tag{6.74}$$

with b_{ik} defined in (6.8). The linearized system is associated with zero boundary conditions and nonzero initial conditions and matching conditions (4.4,4.5-a)-(4.7) as discussed in Chapter IV.

Using the following transformation

$$\begin{bmatrix} v_{1j} \\ v_{2j} \end{bmatrix} = \begin{bmatrix} r \cosh st & \sinh st \\ -\sinh st & -1/r \cosh st \end{bmatrix} \begin{bmatrix} Z_{1j} \\ Z_{2j} \end{bmatrix} \exp\left(\frac{U}{2D} x - \frac{U^2}{4D} t\right) \tag{6.75}$$

the system (6.74) transforms to (4.11) with zero boundary conditions and matching conditions (4.13,4.14). Hence the final solution obtained in this case will be given by (4.23) multiplied by $\exp\left(\frac{U}{2D} x - \frac{U^2}{4D} t\right)$. Thus the condition for stability for the equilibrium state is

$$\frac{U^2}{4D} + \bar{\lambda}_1^2 \bar{\lambda}_2^2 - s > 0 \tag{6.76}$$

where $\bar{\lambda}_1$, $\bar{\lambda}_2$ are given by equations (4.26-a) and (4.26-b) showing that longitudinal convection further stabilizes the equilibrium state.

In the case of prey predator model also the effects of convective and dispersive migrations due to finite number of patches in the habitat can be investigated and similar results as pointed out in the case of two patches may be found.

6.6 CONCLUSIONS

In this chapter the linear stability of migrating speci[illegible] in a patchy habitat has been discussed by considering various combinations of convection and dispersion in different patches.

In the case of one dimensional habitat with dispersion only in the last patch, it has been shown for competition model that an inherently unstable equilibrium state becomes stable in all patches in absence of dispersive migration. However, in the case of semi-infinite habitat the migration has no effect on the stability of the equilibrium state even in the presence of dispersion in the last patch. But when this patch is finite, a general condition for stability involving convective velocity and dispersion coefficient has been obtained.

In the case of two dimensional habitat consisting of only two patches, the linear stability of interacting system has been discussed with dispersion only in the last patch while transverse dispersion in both the patches. In the case of competition model, it has been shown that the stability of equilibrium state in the second patch is dependent on the conditions of its stability in the first patch and even if the equilibrium state is stable in the first patch, it may not be so in the second patch. But if the equilibrium state is unstable in the first patch, it would always be unstable in the second patch.

However, in the presence of equal longitudinal convection and dispersion of the species in all the patches, it has been shown that the effect of longitudinal convection is stabilizing in absence of transverse convection.

The case of prey predator model, in all these cases has also been discussed and it has been shown that the equilibrium state is stable with convection and dispersion in patchy habitats.

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CHAPTER VII

EFFECTS OF SELF AND CROSS DISPERSION ON LINEAR AND NONLINEAR STABILITY

7.1 INTRODUCTION

In previous chapters, we have studied the linear stability of equilibrium state of two interacting and migrating species systems in finite and infinite habitats by considering variable dispersion coefficient. However, it may be noted that, biologically, it is more important to study the stability of nonlinear systems even if it cannot be solved by analytical methods. Such nonlinear stability analysis with and without dispersion has been investigated by using Liapunov second method in few cases (Gatto et. al., 1977, Jacob Jorne and Shlomo Carmi, 1977; Gopalsamy et. al., 1980).

Keeping the above in view, in this chapter, we study the linear and nonlinear stability of two interacting and migrating species system by considering density dependent self and cross dispersion in a finite two-dimensional habitat.

7.2 BASIC EQUATIONS

A general model for the evolution of two interacting and migrating species in a habitat, $0 \leq x \leq L$, $0 \leq y \leq B$, in absence of convection, can be written as [see Chapter II],

$$\frac{\partial u_1}{\partial t} = f_1(u,u_2) + \frac{\partial}{\partial x}\left[D_{1x}(u_1)\frac{\partial u_1}{\partial x} + d_{1x}\frac{\partial u_2}{\partial x}\right] + \frac{\partial}{\partial y}\left[D_{1y}(u_1)\frac{\partial u_1}{\partial y} + d_{1y}\frac{\partial u_2}{\partial y}\right] \tag{7.1}$$

$$\frac{\partial u_2}{\partial t} = f_2(u_1,u_2) + \frac{\partial}{\partial x}\left[D_{2x}(u_2)\frac{\partial u_2}{\partial x} + d_{2x}\frac{\partial u_1}{\partial x}\right] + \frac{\partial}{\partial y}\left[D_{2y}(u_2)\frac{\partial u_2}{\partial y} + d_{2y}\frac{\partial u_1}{\partial y}\right]$$

where u_i, $i=1,2$, the density; (D_{ix}, D_{iy}) the self dispersion coefficient and (d_{ix}, d_{iy}) the cross dispersion coefficient and $f_i(u_1,u_2)$ is the interaction function of the i^{th} species. It has been assumed that D_{ix}, D_{iy}; $i=1,2$ are positive functions of u_1,u_2 while d_{ix}, d_{iy}; $i=1,2$ are constants which may be positive or negative depending upon the type of interaction between the species.

The positive uniform nontrivial equilibrium state $(\bar{u}_1,\bar{u}_2)$ for the system (7.1) can be obtained by solving

$$f_i(\bar{u}_1,\bar{u}_2) = 0\ ; \quad i=1,2$$

using the transformation,

$$u_i = \bar{u}_i + v_i\ ; \quad i=1,2$$

the system (7.1) can be written as

$$\frac{\partial v_1}{\partial t} = f_1(\bar{u}_1+v_1,\bar{u}_2+v_2) + \frac{\partial}{\partial x}\left[D_{1x}(\bar{u}_1+v_1)\frac{\partial v_1}{\partial x} + d_{1x}\frac{\partial v_2}{\partial x}\right] \tag{7.2}$$

$$+ \frac{\partial}{\partial y}\left[D_{1y}(\bar{u}_1+v_1)\frac{\partial v_1}{\partial y} + d_{1y}\frac{\partial v_2}{\partial y}\right]$$

$$\frac{\partial v_2}{\partial t} = f_2(\bar{u}_1+v_1,\bar{u}_2+v_2) + \frac{\partial}{\partial x}\left[D_{2x}(\bar{u}_2+v_2)\frac{\partial v_2}{\partial x} + d_{2x}\frac{\partial v_1}{\partial x}\right]$$

$$+ \frac{\partial}{\partial y}\left[D_{2y}(\bar{u}_2+v_2)\frac{\partial v_2}{\partial y} + d_{2y}\frac{\partial v_1}{\partial y}\right]$$

Linearizing (7.2) we get

$$\frac{\partial v_1}{\partial t} = \sum_{k=1}^{2} b_{1k}v_k + D_{1x}(\bar{u}_1)\,\frac{\partial^2 v_1}{\partial x^2} + D_{1y}(\bar{u}_1)\,\frac{\partial^2 v_1}{\partial y^2} + d_{1x}\,\frac{\partial^2 v_2}{\partial x^2} + d_{2y}\,\frac{\partial^2 v_2}{\partial y^2}$$

$$(7.3)$$

$$\frac{\partial v_2}{\partial t} = \sum_{k=1}^{2} b_{2k}v_k + D_{2x}(\bar{u}_2)\,\frac{\partial^2 v_2}{\partial x^2} + D_{2y}(\bar{u}_2)\,\frac{\partial^2 v_2}{\partial y^2} + d_{2x}\,\frac{\partial^2 v_1}{\partial x^2} + d_{2y}\,\frac{\partial^2 v_1}{\partial y^2}$$

where,

$$b_{ik} = \left(\frac{\partial f_i}{\partial u_k}\right)\bar{u}_1,\bar{u}_2 \quad ; \; i,k = 1,2$$

It can be noted here that in the linearized system (7.3), the self dispersion coefficients are now functions of equilibrium state and would be constants for fixed $(\bar{u}_1,\bar{u}_2)$.

The following initial boundary conditions are associated with the system (7.2) or (7.3)

$$v_i(x,y,0) = F_i(x,y) \qquad (7.4)$$

$$\begin{aligned} v_i(0,y,t) &= 0 \\ v_i(L,y,t) &= 0 \\ v_i(x,0,t) &= 0 \\ v_i(x,B,t) &= 0 \end{aligned} \qquad (7.5)$$

In the following we discuss the linear and nonlinear stability of equilibrium state in cases of competition and prey predator models.

7.3 COMPETITION MODEL

In case of competing species the interaction functions are written as

$$\begin{aligned} f_1 &= u_1(a_1 - b_1u_1 - c_1u_2) \\ f_2 &= u_2(a_2 - b_2u_2 - c_2u_1) \end{aligned} \tag{7.6}$$

The positive equilibrium state of the system (7.2), (7.3) with (7.6) can be obtained as

$$\bar{u}_1 = \frac{a_1b_2 - c_1a_2}{b_1b_2 - c_1c_2} \quad ; \quad \bar{u}_2 = \frac{a_2b_1 - c_2a_1}{b_1b_2 - c_1c_2}$$

provided,

$$\frac{b_1}{c_2} > \frac{a_1}{a_2} > \frac{c_1}{b_2} \tag{7.7-a}$$

or,

$$\frac{b_1}{c_2} < \frac{a_1}{a_2} < \frac{c_1}{b_2} \tag{7.7-b}$$

The corresponding linear system is given by (7.3) with

$$\begin{aligned} b_{11} &= -b_1\bar{u}_1 < 0 \quad ; \quad b_{12} = -c_1\bar{u}_1 < 0 \\ b_{21} &= -c_2\bar{u}_2 < 0 \quad ; \quad b_{22} = -b_2\bar{u}_2 < 0 \end{aligned} \tag{7.8}$$

7.3.1 DISCUSSION OF LINEAR STABILITY

To discuss the linear stability of the system (7.3) about the equilibrium state $(\bar{u}_1, \bar{u}_2)$, let us choose a positive definite function, E, in the first quadrant, as

$$E = \frac{1}{2} \int_0^B \int_0^L (v_1^2 + cv_2^2)\, dx\, dy \tag{7.9}$$

where c is a positive constant to be determined.

From (7.3) and (7.9), dE/dt is obtained as

$$\begin{aligned}\frac{dE}{dt} &= \int_0^B \int_0^L \left[b_{11}v_1^2 + cb_{22}v_2^2 + (b_{12}+cb_{21})\, v_1 v_2\right] dxdy \\ &+ \int_0^B \int_0^L \left[D_{1x}v_1 \frac{\partial^2 v_1}{\partial x^2} + D_{1y}v_1 \frac{\partial^2 v_1}{\partial y^2} + cD_{2x}v_2 \frac{\partial^2 v_2}{\partial x^2} + cD_{2y}v_2 \frac{\partial^2 v_2}{\partial y^2}\right. \\ &\quad + d_{1x}v_1 \frac{\partial^2 v_2}{\partial x^2} + d_{1y}v_1 \frac{\partial^2 v_2}{\partial y^2} + cd_{2x}v_2 \frac{\partial^2 v_1}{\partial x^2} \\ &\quad \left. + cd_{2y}v_2 \frac{\partial^2 v_1}{\partial y^2}\right] dxdy\end{aligned} \tag{7.10}$$

Using zero reservoir boundary conditions (7.5) around the habitat the second term on the R.H.S. of (7.10) can be simplified giving

$$\begin{aligned}\frac{dE}{dt} &= \int_0^B \int_0^L \left[b_{11}v_1^2 + cb_{22}v_2^2 + (b_{12}+cb_{21})\, v_1 v_2\right] dxdy \\ &- \int_0^B \int_0^L \left[D_{1x}\left(\frac{\partial v_1}{\partial x}\right)^2 + D_{1y}\left(\frac{\partial v_1}{\partial y}\right)^2 + c\left\{D_{2x}\left(\frac{\partial v_2}{\partial x}\right)^2 + D_{2y}\left(\frac{\partial v_2}{\partial y}\right)^2\right\}\right. \\ &+ \left.(d_{1x}+cd_{2x})\left(\frac{\partial v_1}{\partial x}\right)\left(\frac{\partial v_2}{\partial x}\right) + (d_{1y}+cd_{2y})\left(\frac{\partial v_2}{\partial y}\right)\left(\frac{\partial v_1}{\partial y}\right)\right] dxdy\end{aligned} \tag{7.11}$$

Denoting

$$P = b_{11}v_1^2 + cb_{22}v_2^2 + (b_{12}+cb_{21})\, v_1 v_2 \tag{7.12}$$

$$Q = D_{1x}\left(\frac{\partial v_1}{\partial x}\right)^2 + D_{1y}\left(\frac{\partial v_1}{\partial y}\right)^2 + c\left[D_{2x}\left(\frac{\partial v_2}{\partial x}\right)^2 + D_{2y}\left(\frac{\partial v_2}{\partial y}\right)^2\right]$$

$$+ (d_{1x}+cd_{2x})\left(\frac{\partial v_1}{\partial x}\right)\left(\frac{\partial v_2}{\partial x}\right) + (d_{1y}+cd_{2y})\left(\frac{\partial v_1}{\partial y}\right)\left(\frac{\partial v_2}{\partial y}\right) \qquad (7.13)$$

we get from (7.11),

$$\frac{dE}{dt} = \int_0^B \int_0^L P\,dxdy - \int_0^B \int_0^L Q\,dxdy \qquad (7.14)$$

In absence of dispersion, it can be noted from (7.12) that E is a Liapunov function provided the quadratic P is negative definite, the condition for which is obtained as

$$b_{11}b_{22}-b_{12}b_{21} > (b_{12}-cb_{21})^2 \geq 0 \qquad (7.15)$$

choosing $c = c_1/c_2$ we get the necessary and sufficient condition for stability of the equilibrium state without dispersion, after using (7.8) as

$$b_1b_2 - c_1c_2 > 0 \qquad (7.16)$$

In the case of dispersion, when the condition (7.16) is satisfied, it can be seen from (7.14) that for E to be a Liapunov function, the other quadratic Q should also be positive definite, the conditions for which are obtained as

$$4c\, D_{1x}D_{2x} > (d_{1x} + cd_{2x})^2$$

and $\qquad (7.17)$

$$4c\, D_{1y}D_{2y} > (d_{1y} + cd_{2y})$$

which can be rewritten as

$$4c(D_{1x}D_{2x}-d_{1x}d_{2x}) > (d_{1x}-cd_{2x})^2 \geq 0$$

and (7.18)

$$4c(D_{1y}D_{2y}-d_{1y}d_{2y}) > (d_{1y}-cd_{2y})^2 \geq 0$$

Since D_{ix}, D_{iy} ; $i=1,2$ are positive, these conditions ~~would~~ may be satisfied provided one of the following holds good.

i. $$|d_{1x}\ d_{2x}| < |D_{1x}\ D_{2x}|$$
$$|d_{1y}\ d_{2y}| < |D_{1y}\ D_{2y}| \qquad (7.19\text{-a})$$

ii. $$d_{1x}\ d_{2x} \leq 0$$
$$d_{1y}\ d_{2y} \leq 0 \qquad (7.19\text{-b})$$

Thus, as in this case the cross dispersion coefficients of both the species are positive, the condition for linear stability of an otherwise stable equilibrium state is given by (7.19-a). However, in the absence of cross dispersion the otherwise stable equilibrium state remains so with self dispersion.

In the case when the quadratic P is not negative definite i.e. the condition (7.15) is not satisfied then with positive definite quadratic Q (i.e. the condition (7.19) is satisfied), there exist a possibility for which dE/dt may become negative definite. In the following we find the conditions for which E becomes a Liapunov function in such a case.

As pointed out earlier the cross dispersion coefficients for competing species are positive, the expression for dE/dt can then be further, simplified to give

$$\frac{dE}{dt} = \int_0^B \int_0^L \left[P - Q_1\right] dxdy \tag{7.20}$$

where

$$Q_1 = (D_{1x} - \frac{G_x}{2})(\frac{\partial v_1}{\partial x})^2 + (D_{2x}c - \frac{G_x}{2})(\frac{\partial v_2}{\partial x})^2 + \frac{G_x}{2}\{\frac{\partial}{\partial x}(v_1+v_2)\}^2$$
$$+ (D_{1y} - \frac{G_y}{2})(\frac{\partial v_1}{\partial y})^2 + (D_{2y}c - \frac{G_y}{2})(\frac{\partial v_2}{\partial y})^2 + \frac{G_y}{2}\{\frac{\partial}{\partial y}(v_1+v_2)\}^2 \tag{7.21}$$

$$G_x = d_{1x} + cd_{2x}$$

and

$$G_y = d_{1y} + cd_{2y} \tag{7.22}$$

considering the case

$$D_{1x} > G_x \quad ; \quad cD_{2x} > G_x$$
$$D_{1y} > G_y \quad ; \quad cD_{2y} > Gy \tag{7.23}$$

for which the conditions (7.18) and so (7.19) also are consistent and using the Poincare's inequality (Denn, 1975), (7.21) is simplified as follows.

$$\frac{dE}{dt} \leq \int_0^B \int_0^L \left[(b_{11}-\sigma_1)v_1^2 + (cb_{22}-\sigma_2)\, v_2^2 + (b_{12}+cb_{21}-G)\, v_1 v_2\right] dxdy \tag{7.24}$$

where

$$G = \rho_1 + c\rho_2 \tag{7.25}$$

$$\rho_i = d_{ix}\frac{\pi^2}{L^2} + d_{iy}\frac{\pi^2}{B^2}$$
$$\sigma_i = D_{ix}\frac{\pi^2}{L^2} + D_{iy}\frac{\pi^2}{B^2} \tag{7.26}$$

It can be noted from (7.24) that the function E is a Liapunov function provided

$$b_{11}b_{22}-b_{12}b_{21}-(b_{11}\sigma_2+h_{22}\sigma_1) + (b_{12}\rho_2+b_{21}\rho_1)$$
$$+ \left(\sigma_1\sigma_2 - \frac{G^2}{4c}\right) > 0 \tag{7.27}$$

It can be seen from (7.25) that

$$G^2 > 4c\,\rho_1\rho_2 \tag{7.28}$$

and thus the condition for stability (7.27) takes the following form:

$$b_{11}b_{22}-b_{12}b_{21}-(b_{11}\sigma_2+b_{22}\sigma_1) + (b_{12}\rho_2+b_{21}\rho_1)$$
$$+ (\sigma_1\sigma_2-\rho_1\rho_2) > 0 \tag{7.29}$$

under (7.23)

It can be remarked here that the condition (7.29) is necessary and sufficient for the stability of the equilibrium state under (7.23). Thus the equilibrium state which is stable or unstable with or without self dispersion would become stable with cross dispersion under (7.23) provided the condition (7.29) is satisfied.

7.3.2 DISCUSSION OF NONLINEAR STABILITY

To discuss the nonlinear stability of the equilibrium state of the system (7.2), consider the following positive definite function in the domain $u_1 = \bar{u}_1 + v_1 > 0$, $u_2 = \bar{u}_2 + v_2 > 0$

$$V = \int_0^B \int_0^L \left[v_1 - \bar{u}_1 \ln\left(1 + \frac{v_1}{\bar{u}_1}\right) + c\left\{ v_2 - \bar{u}_2 \ln\left(1 + \frac{v_2}{\bar{u}_2}\right)\right\}\right] dxdy \tag{7.30}$$

where c is a positive constant defined as before.

In the following we find the condition for the function V to be a Liapunov function providing the sufficient conditions for the nonlinear stability of the equilibrium state for the system (7.2) with (7.8).

Let us first prescribe the function for the self dispersion coefficients (D_{ix}, D_{iy}) $i=1,2$ as

$$\left.\begin{aligned} D_{ix} &= \bar{D}_{ix} = c_{ii} u_i \\ D_{iy} &= \bar{D}_{iy} + e_{ii} u_i \end{aligned}\right\} ;\ i=1,2 \tag{7.31}$$

where c_{ii}, e_{ii} are positive constants.

The time derivative of, V, can be obtained as

$$\frac{dV}{dt} = \int_0^B \int_0^L \left[\frac{v_1}{v_1+\bar{u}_1} \frac{\partial v_1}{\partial t} + \frac{cv_2}{v_2+\bar{u}_2} \frac{\partial v_2}{\partial t} \right] dxdy \tag{7.32}$$

Substitution of (7.2) in (7.32) would give

$$\frac{dV}{dt} = - \iint (\bar{P} + \bar{Q})\, dxdy \tag{7.33}$$

where

$$\bar{P} = b_1 v_1^2 + cb_2 v_2^2 + (c_1+cc_2)\, v_1 v_2 \tag{7.34}$$

$$\bar{Q} = \bar{u}_1 \{\frac{\bar{D}_{1x}}{(v_1+\bar{u}_1)^2} + \frac{c_{11}}{(v_1+\bar{u}_1)}\} (\frac{\partial v_1}{\partial x})^2 + \bar{u}_1 \{\frac{\bar{D}_{1y}}{(v_1+\bar{u}_1)^2} + \frac{e_{11}}{(v_1+\bar{u}_1)}\}(\frac{\partial v_1}{\partial y})^2$$
$$+ c\bar{u}_2\{\frac{\bar{D}_{2x}}{(v_2+\bar{u}_2)^2} + \frac{c_{22}}{v_2+\bar{u}_2}\} (\frac{\partial v_2}{\partial x})^2 \}+\bar{u}_2 c \{\frac{\bar{D}_{2y}}{(v_2+\bar{u}_2)^2} + \frac{e_{22}}{v_2+\bar{u}_2}\} (\frac{\partial v_2}{\partial y})^2$$
$$+ \{\frac{\bar{u}_1 d_{1x}}{(u_1+\bar{u}_1)^2} + \frac{c\bar{u}_2 d_{2x}}{(v_2+\bar{u}_2)^2}\} (\frac{\partial v_1}{\partial x})(\frac{\partial v_2}{\partial x}) + \{\frac{\bar{u}_1 d_{1y}}{(v_1+\bar{u}_1)^2} + \frac{c\bar{u}_2 d_{2y}}{(u_2+\bar{u}_2)^2}\}$$
$$(\frac{\partial v_1}{\partial y})(\frac{\partial v_2}{\partial y}) \tag{7.35}$$

In the absence of dispersion, it can be noted from (7.34) that V is a Liapunov function provided the condition (7.16) is satisfied giving the condition for nonlinear stability of the equilibrium state, which is the same as obtained for the linear stability.

In the case with dispersion, it can be noted that if the quadrative $\bar{Q}$ is also positive definite then V is a Liapunov function (with self and cross dispersion) the conditions for which are obtained as

$$\bar{u}_1\bar{u}_2 \Big[\frac{\bar{D}_{1x}\bar{D}_{2x}-d_{1x}d_{2x}}{(v_1+\bar{u}_1)^2(v_2+\bar{u}_2)^2} + \frac{c_{11}c_{22}}{(v+\bar{u}_1)(v_2+\bar{u}_2)} + \frac{c_{11}\bar{D}_{2x}}{(u_1+\bar{u}_1)(v_2+\bar{u}_2)^2}$$
$$+ \frac{c_{22}\bar{D}_{1x}}{(v_1+\bar{u}_2)^2(v_2+\bar{u}_2)}\Big] > Q. \tag{7.36-a}$$

and

$$\bar{u}_1\bar{u}_2 \left[\frac{\bar{D}_{1y}\bar{D}_{2y}-d_{1y}d_{2y}}{(v_1+\bar{u}_1)^2(v_2+\bar{u}_2)^2} + \frac{e_{11}e_{22}}{(v_1+\bar{u}_1)(v_2+\bar{u}_2)} + \frac{e_{11}\bar{D}_{2y}}{(v_1+\bar{u}_1)(v_2+\bar{u}_2)^2} + \frac{e_{22}\bar{D}_{1y}}{(v_1+\bar{u}_1)^2(v_2+u_2)} \right] > 0 \qquad (7.36\text{-a})$$

which are satisfied provided,

$$\begin{aligned} \bar{D}_{1x}\bar{D}_{2x}-d_{1x}d_{2x} &> 0 \\ \bar{D}_{1y}\bar{D}_{2y}-d_{1y}d_{2y} &> 0 \end{aligned} \qquad (7.36\text{-b})$$

As these are also the conditions for linear stability of the equilibrium state, it is concluded that the sufficient condition for nonlinear stability of equilibrium state with dispersion is that it is linear stable with dispersion.

If the condition (7.5) is not satisfied, then it can be noted from (7.33) that under the condition (7.36), there exists a possibility for which the function V becomes a Liapunov function in a subregion of the positive quadrant. For this let us choose positive constants U_o, V_o such that

$$U_o > \bar{u}_1 \; ; \quad V_o > \bar{u}_2$$

In the region $A = \{(u_1,u_2): u_1 \leq V_o,\ u_2 \leq V_o\}$. The expression for dV/dt (7. 33) simplifies to

$$\frac{dV}{dt} < - \int_0^B \int_0^L (\bar{P} + \bar{Q}_1)\, dxdy \qquad (7.37)$$

where

$$\bar{Q}_1 = \frac{u_1}{U_o^2}(\bar{D}_{1x}+c_{11}U_o)\left(\frac{\partial v_1}{\partial x}\right)^2 + \frac{\bar{u}_1}{U_o^2}(\bar{D}_{1y}+e_{11}U_o)\left(\frac{\partial v_1}{\partial y}\right)^2$$

$$+ \frac{C\bar{u}_2}{V_o^2}(\bar{D}_{2x}+c_{22}V_o)\left(\frac{\partial v_2}{\partial x}\right)^2 + \frac{c\bar{u}_2}{V_o^2}(\bar{D}_{2y}+ e_{22}V_o)\left(\frac{\partial v_2}{\partial y}\right)^2$$

$$+ \left(\frac{\bar{u}_1 d_{1x}}{U_o^2} + \frac{c\bar{u}_2 d_{2x}}{V_o^2}\right)\left(\frac{\partial v_1}{\partial x}\right)\left(\frac{\partial v_2}{\partial x}\right) + \left(\frac{\bar{u}_1 d_{1y}}{U_o^2} + \frac{c\bar{u}_2 d_{2y}}{V_o^2}\right)\left(\frac{\partial v_1}{\partial y}\right)\left(\frac{\partial v_2}{\partial y}\right) \tag{7.38}$$

As discussed before (d_{ix}, d_{iy}) ; $i=1,2$ are both positive in this case $\bar{Q}_1$ becomes

$$\bar{Q}_1 = \left\{\frac{\bar{u}_1}{U_o^2}(\bar{D}_{1x}+c_{11}U_o) - \frac{K_x}{2}\right\}\left(\frac{\partial v_1}{\partial x}\right)^2 + \left\{\frac{\bar{u}_1}{U_o^2}(\bar{D}_{1y}+e_{11}U_o) - \frac{K_y}{2}\right\}\left(\frac{\partial v_1}{\partial y}\right)^2$$

$$+ \left\{\frac{c\bar{u}_2}{V_o^2}(\bar{D}_{2x}+c_{22}V_o) - \frac{K_x}{2}\right\}\left(\frac{\partial v_2}{\partial x}\right)^2 + \left\{\frac{c\bar{u}_2}{V_o^2}(\bar{D}_{2y}+e_{22}V_o) - \frac{K_y}{2}\right\}\left(\frac{\partial v_2}{\partial y}\right)^2$$

$$+ \frac{K_x}{2}\frac{\partial}{\partial x}\{(v_1+v_2)\}^2 + \frac{K_y}{2}\left\{\frac{\partial}{\partial x}(v_1+v_2)\right\}^2 . \tag{7.39}$$

where

$$K_x = \frac{\bar{u}_1 d_{1x}}{U_o^2} + \frac{c\bar{u}_2 d_{2x}}{V_o^2}$$
$$K_y = \frac{\bar{u}_1 d_{1y}}{U_o^2} + \frac{c\bar{u}_2 d_{2y}}{V_o^2} \tag{7.40}$$

considering the case

$$\frac{\bar{u}_1}{U_o^2}(\bar{D}_{1x}+c_{11}U_o) > K_x \; ; \; \frac{\bar{u}_1}{U_o^2}(\bar{D}_{1y}+ e_{11}U_o) > K_y$$
$$\frac{c\bar{u}_2}{V^2}(\bar{D}_{2x}+c_{22}V_o) > K_x \; ; \; \frac{c\bar{u}_2}{V^2}(\bar{D}_{2y}+e_{22}V_o) > K_y \tag{7.41}$$

for which the conditions (7.36) are consistent, we get after using Poincare's inequality

$$\frac{dV}{dt} = -\int_0^B\int_0^L \Big[(b_1 + \frac{\bar{u}_1}{U_o^2}\,\sigma_1 + \frac{\bar{u}_1}{U_o}\,w_1)\,v_1^2 + c(b_2 + \frac{\bar{u}_2}{V_o^2}\,\sigma_2 + \frac{\bar{u}_2}{V_o}\,w_2)\,v_2^2$$

$$+ (c_1 + cc_2 + K)v_1 v_2 \Big]\,dxdy \qquad (7.42)$$

where

$$w_i = c_{ii}\,\frac{\pi^2}{L^2} + e_{ii}\,\frac{\pi^2}{B^2}$$

$$K = \frac{\bar{u}_1}{U_o^2}\,\rho_1 + \frac{c\bar{u}_2}{V_o^2}\,\rho_2 \qquad (7.43)$$

Thus, the condition for stability of the equilibrium state can be obtained as follows

$$b_1 b_2 - c_1 c_2 + b_2\bar{u}_1(\frac{\sigma_1}{U_o^2} + \frac{w_1}{U_o}) + \bar{u}_2 b_1\,(\frac{\sigma_2}{V_o^2} + \frac{w_2}{V_o})$$

$$+ \bar{u}_1\bar{u}_2(\frac{\sigma_1}{U_o^2} + \frac{w_1}{U_o})(\frac{\sigma_2}{V_o^2} + \frac{w_2}{V_o}) - (\frac{c_2\bar{u}_1}{V_o^2}\,\rho_1 + \frac{c_1\bar{u}_2}{V_o^2}\,\rho_2)$$

$$- \frac{\bar{u}_1\bar{u}_2\rho_1\rho_2}{U_o^2\,V_o^2} > 0 \qquad (7.44)$$

Thus, it can be concluded that (7.44) is the sufficient condition for nonlinear stability of the equilibrium state with dispersion in a region A under (7.41) even if (7.5) is not satisfied. As (7.44) determines the region A, it may be pointed out that the region of stability increases with increasing self dispersion (constant) and decreasing cross dispersion.

7.4 PREY-PREDATOR MODEL

In the case of prey predator model, the Volterra type of interaction functions are given by

$$
\begin{aligned}
f_1(u_1,u_2) &= (a_1-b_1u_1-c_1u_2)\, u_1 \\
f_2(u_1,u_2) &= (-a_2-b_2u_2+c_2u_1)u_2
\end{aligned}
\tag{7.45}
$$

which gives the positive equilibrium state as follows:

$$
\frac{a_2c_1 + a_1b_2}{a_1c_2 + b_1b_2} \, , \, \frac{a_1c_2-a_2b_1}{c_1c_2+b_1b_2}
$$

provided $a_1c_2-a_2b_1 > 0$. The linearized system can be given by (7.3) with

$$
\begin{aligned}
b_{11} &= -b_1\bar{u}_1 < 0 \qquad & b_{12} &= -c_1\bar{u}_1 < 0 \\
b_{21} &= +c_2\bar{u}_2 < 0 \qquad & b_{22} &= -b_2\bar{u}_2 > 0
\end{aligned}
\tag{7.46}
$$

To see the linear stability of the equilibrium state, the same positive definite function E is considered from which, proceeding as before, it can be noted that E given by (7.9) is a Liapunov function in the absence of dispersion, as the condition (7.16) is always satisfied. Thus, in the case of prey predator model the equilibrium state is nonlinearly stable without dispersion. Further, in presence of self and cross dispersion the quadratic Q remains the same as before and the condition (7.19) for positive definiteness of Q is always satisfied as the cross dispersion coefficients for the prey

predator species are of opposite signs (Kerner, 1959). Thus it is concluded that prey predator model is linearly stable with self and cross dispersion.

To investigate the nonlinear stability of the equilibrium state, choosing the same Liapunov function as (7.30) and proceeding, as in the case of competition model, it can be concluded that prey predator model is nonlinearly stable with or without dispersion.

7.5 CONCLUSIONS

In this chapter, the linear and nonlinear stability of uniform positive equilibrium state for both competition and prey predator models have been investigated by the Liapunov second method.

The following results have been obtained in the case of competition model.

1. The linearly stable equilibrium state remains stable with self dispersion. The necessary and sufficient conditions for the stable equilibrium state to remain stable with cross dispersion also has been obtained.

2. The equilibrium state which is otherwise linearly unstable may become stable with dispersion (self and cross) under condition (7.29) for the case (7.23).

3. In absence of dispersion the linearly stable equilibrium

state remains nonlinearly stable.

4. In presence of dispersion it has been shown that the equilibrium state is nonlinearly stable in positive quadrant (u_1, u_2) provided it is linearly stable with and without dispersion.

5. However, if the equilibrium state is linearly unstable without dispersion which becomes linearly stable with dispersion (self and cross) in positive quadrant, then it is possible to determine a subregion where the equilibrium state is nonlinearly stable and the region of stability increases with increasing self dispersion and decreasing cross dispersion.

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CHAPTER VIII

EFFECTS OF PATCHINESS ON LINEAR AND NONLINEAR STABILITY

8.1 INTRODUCTION

In the previous chapter, the linear and nonlinear stability of the equilibrium state has been studied with density dependent dispersal using Liapunov second method. As pointed out in Chapter IV, the dispersal coefficient may also vary with space and such effect on stability can be studied by considering the patchiness of the habitat.

Keeping this in view, in this chapter, we study the linear and nonlinear stability of the equilibrium state of competition and prey predator models in a two dimensional finite patchy habitat.

8.2 BASIC EQUATIONS

Assuming the habitat to be consisting of finitely many patches (say N) such that the j^{th} patch is defined as $L_{j-1} < x < L_j$; $j=1,2,\ldots,N$ with $L_0=0$ and $L_N = L$, the system governing the evolution of two interacting, dispersing species in j^{th} patch can be written as

$$\frac{\partial u_{ij}}{\partial t} = f_{ij} + D_{ijx} \frac{\partial^2 u_{ij}}{\partial x^2} + D_{ijy} \frac{\partial^2 u_{ij}}{\partial y^2} \tag{8.1}$$

$$i = 1,2; \; j = 1,2,\ldots, N.$$

where u_{ij}, (D_{ijx}, D_{ijy}), f_{ij} denote the density, dispersion coefficient and the interaction function of i^{th} species in j^{th} patch. As before the interaction coefficients of the species have been assumed to be unaffected by the patchiness of the habitat and then the uniform positive equilibrium state $(\bar{u}_1,\bar{u}_2)$ is obtained by solving

$$f_{ij}\ (\bar{u}_1,\bar{u}_2) = 0$$

Writing

$$u_{ij} = \bar{u}_i + v_{ij}$$

in (8.1) we get the non-linear form as

$$\frac{\partial v_{ij}}{\partial t} = f_{ij}(\bar{u}_1+v_{ij},\ \bar{u}_2+v_{2j}) + D_{ijx}\frac{\partial^2 v_{ij}}{\partial x^2} + D_{ijy}\frac{\partial^2 v_{ij}}{\partial y^2} \qquad (8.2)$$

and the corresponding linearized system as

$$\frac{\partial v_{ij}}{\partial t} = \sum_{k=1}^{2} b_{ik}v_{kj} + D_{ijx}\frac{\partial^2 v_{ij}}{\partial x^2} + D_{ijy}\frac{\partial^2 v_{ij}}{\partial y^2} \qquad (8.3)$$

where

$$b_{ik} = \left(\frac{\partial f_{ij}}{\partial u_{kj}}\right)\bar{u}_1,\bar{u}_2\ .$$

The system (8.2) and (8.3) are associated with the following initial, boundary and matching conditions.

i Initial conditions :

$$v_{ij}(x,y,0) = F_{ij}(x) \qquad (8.4\text{-a})$$

such that $F_{ij}(L_{j-1}) = F_{i(j-1)}(L_{j-1})$ (8.4-b)

(ii) Boundary conditions :

$$
\begin{aligned}
v_{i1}\ (0,y,t) &= 0 \\
v_{iN}\ (L,y,t) &= 0 \\
v_{ij}\ (x,0,t) &= 0 \\
v_{ij}\ (x,B,t) &= 0
\end{aligned}
\tag{8.5}
$$

(iii) Matching conditions :

$$v_{ij}\ (L_{j-1},y,t) = v_{i(j-1)}\ (L_{j-1},y,t) \tag{8.6}$$

$$D_{ij}\ \left(\frac{\partial v_{ij}}{\partial x}\right) = D_{i(j-1)}\ \left(\frac{\partial v_{i(j-1)}}{\partial x}\right) \quad \text{at} \quad x = L_{j-1} \tag{8.7}$$

for $i=1,2$; $j = 2,\ldots,N$.

In the following, we discuss the linear and nonlinear stability of equilibrium state in the cases of competition and prey predator models separately using the Liapunov second method.

8.3 COMPETITION MODEL

The interaction function for competing species including crowding effects can be written as follows:

$$
\begin{aligned}
f_{1j} &= u_{1j}(a_1-b_1u_{1j}-c_1u_{2j}) \\
f_{2j} &= u_{2j}(a_2-b_2u_{2j}-c_2u_{1j})
\end{aligned}
\tag{8.8}
$$

which give the positive uniform equilibrium state for the systems (8.2), (8.3) as

$$\bar{u}_1 = \frac{a_1b_2-c_1a_2}{b_1b_2-c_1c_2}\ ; \quad \bar{u}_2 = \frac{a_2b_1-c_2a_1}{b_1b_2-c_1c_2}$$

provided

$$\frac{b_1}{c_2} > \frac{a_1}{a_2} > \frac{c_1}{b_2} \tag{8.9}$$

$$\frac{b_1}{c_2} < \frac{a_1}{a_2} < \frac{c_1}{b_2} \tag{8.10}$$

The corresponding linearized system is given by (8.3) with

$$\begin{aligned} b_{11} &= -b_1\bar{u}_1 < 0 \; ; \; b_{12} = -c_1\bar{u}_1 < 0 \\ b_{21} &= -c_2\bar{u}_2 < 0 \; ; \; b_{22} = -b_2\bar{u}_2 < 0 \end{aligned} \tag{8.11}$$

8.3.1 DISCUSSION OF LINEAR STABILITY

To discuss the linear stability, we choose the positive definite function E, as

$$E = \frac{1}{2}\int_0^L \int_0^B \left[v_1^2 + cv_2^2 \right] dxdy \tag{8.12}$$

where $v_i = v_{ij}$ for $L_{j-1} < x < L_j$, $j=1,2,\ldots,N$

and c is a positive constant to be determined.

From (8.3) the time derivative of E is obtained as

$$\begin{aligned} \frac{dE}{dt} = \int_0^B \sum_{j=1}^{N} \int_{L_{j-1}}^{L_j} \Big[& b_{11}v_{1j}^2 + cb_{22}v_{2j}^2 + (b_{12}+cb_{21})\, v_{1j}v_{2j} \\ & - D_{1jx}\left(\frac{\partial v_{1j}}{\partial x}\right)^2 - cD_{2jx}\left(\frac{\partial v_{2j}}{\partial x}\right)^2 \\ & - D_{1jy}\left(\frac{\partial v_{1j}}{\partial y}\right)^2 - cD_{2jy}\left(\frac{\partial v_{2j}}{\partial y^2}\right)^2 \Big] \end{aligned} \tag{8.13}$$

after using (8.11) and conditions (8.5)-(8.7).

It can be seen from (8.13) that in absence of dispersion, dE/dt is negative definite provided,

$$b_1 b_2 - c_1 c_2 > 0 \tag{8.14}$$

obtained after using Sylvester conditions and choosing $c = c_1/c_2$. The condition (8.14) assures the existence of Liapunov function in absence of dispersion and gives the necessary and sufficient conditions for stability in absence of dispersion.

It can be noted from (8.13) that the equilibrium state which is stable otherwise remains so with dispersion in patchy habitat also.

In case, when condition (8.14) is not satisfied, let us explore the possibility for which E is still a Liapunov function with dispersion.

For this, using the inequality (A10) obtained in the Appendix, the expression (8.13) for dE/dt simplifies to

$$\frac{dE}{dt} \leq \int_0^B \int_0^L \left[(b_{11} - \bar{\lambda}_1^2)\, v_1^2 + c(b_{22} - \bar{\lambda}_2^2)\, v_2^2 + (b_{12} + c b_{21}) v_1 v_2\right] dxdy \tag{8.15}$$

which shows that dE/dt is negative definite provided

$$b_{11} b_{22} - b_{12} b_{21} - b_{11} \bar{\lambda}_2^2 - b_{22} \bar{\lambda}_1^2 + \bar{\lambda}_1^2 \bar{\lambda}_2^2 > 0 \tag{8.16}$$

where $\bar{\lambda}_i$; $i=1,2$ are the roots of the equation obtained after simplifying (A6) and (A9). It is noted that if the condition (8.16) is satisfied for minimum roots of $\bar{\lambda}_i^2$; $i=1,2$,

it would also be satisfied for all the other roots. Thus for minimum values of $\bar{\lambda}_i^2$ $i=1,2$ (8.16) is the necessary and sufficient condition for linear stability of otherwise unstable equilibrium state.

8.3.2 DISCUSSION OF NONLINEAR STABILITY

To investigate the nonlinear stability of the equilibrium state $(\bar{u}_1,\bar{u}_2)$ of the system (8.2), the following positive definite function, in the positive quadrant of u_1,u_2 is considered.

$$V = \int_0^L \int_0^B \left[v_1-\bar{u}_1 \ln(1+\frac{v_1}{\bar{u}_1}) + c\{v_2-\bar{u}_2 \ln(1+\frac{v_2}{\bar{u}_2})\}\right]dxdy \tag{8.17}$$

Using (8.11) we get the time derivative of V as

$$\begin{aligned}\frac{dV}{dt} = -\int_0^B \sum_{j=1}^{N} \int_{L_{j-1}}^{L_j} \Big[& b_1v_1^2+cb_2v_2^2+(c_1+cc_2)v_1v_2 + \\ &+ \frac{\bar{u}_1D_{1jx}}{(\bar{u}_1+v_{1j})^2}\left(\frac{\partial v_{1j}}{\partial x}\right)^2 + \frac{\bar{u}_1D_{1jy}}{(\bar{u}_1+v_{1j})^2}\left(\frac{\partial v_{1j}}{\partial y}\right)^2 \\ &+ \frac{c\bar{u}_2D_{2jx}}{(\bar{u}_2+v_{2j})^2}\left(\frac{\partial v_{2j}}{\partial x}\right)^2 + \frac{c\bar{u}_2D_{2jy}}{(\bar{u}_2+v_{2j})^2}\left(\frac{\partial v_{2j}}{\partial y}\right)^2\Big]dxdy\end{aligned} \tag{8.18}$$

after using boundary conditions (8.5) and matching conditions (8.6). It is seen from (8.18) that as in the case of linear stability, the condition for nonlinear stability of the equilibrium state is given by (8.14) in absence of dispersion.

Thus, the equilibrium state is nonlinearly stable if it is linearly stable without dispersion. Further it can also be noted from (8.18) that the otherwise stable equilibrium state remains stable nonlinearly with dispersion also as D_{ijx}, D_{ijy} are positive for $i=1,2;\ j=1,2...N$.

Even if condition (8.14) is not satisfied, in the following, we find a subregion A of positive quadrant in which the equilibrium state $(\bar{u}_1, \bar{u}_2)$ becomes nonlinearly stable with dispersion.

For this, let us assume $U_{oj}, V_{oj}, j=1,2,...,N$ such that

$$\begin{aligned} u_{1j} &= \bar{u}_1 + v_{1j} < U_{oj} \\ u_{2j} &= \bar{u}_2 + v_{2j} < V_{oj} \end{aligned} \tag{8.19}$$

and $\quad U_{oj} > \bar{u}_1,\ V_{oj} > \bar{u}_2$.

Considering the region $A = \{(u_1, u_2) : u_1 \leq \bar{U}_o,\ U_2 \leq \bar{V}_o\}$ where $\bar{U}_o, \bar{V}_o$ are the maximum values of $U_{oj}, V_{oj};\ j=1,2,...N$ respectively.

The expression (8.18) for dV/dt can now be simplified in the region A to the following form

$$\begin{aligned} \frac{dV}{dt} = -\int_0^B \sum_{j=1}^{N} \int_{L_{j-1}}^{L_j} \Big[& b_1 v_{1j}^2 + cb_2 v_{2j}^2 + (c_1 + cc_2)\, v_{1j} v_{2j} \\ & + \frac{\bar{u}_1 D_{1jx}}{\bar{U}_o^2} \left(\frac{\partial v_{1j}}{\partial x}\right)^2 + \frac{\bar{u}_1 D_{1jy}}{\bar{U}_o^2} \left(\frac{\partial v_{1j}}{\partial y}\right)^2 \\ & + \frac{c\bar{u}_2 D_{2jx}}{\bar{V}_o^2} \left(\frac{\partial v_{2j}}{\partial x}\right)^2 + \frac{c\bar{u}_2 D_{2jy}}{\bar{V}_o^2} \left(\frac{\partial v_{2j}}{\partial y}\right)^2 \Big] dxdy \end{aligned} \tag{8.20}$$

Using the inequality (A10) we get from (8.20)

$$\frac{dV}{dt} \leq -\int_0^B \int_0^L \Big[(b_1 + \frac{\bar{u}_1}{\bar{U}_o^2} \bar{\lambda}_1^2)\, v_1^2 + c(b_2 + \frac{\bar{u}_2}{\bar{V}_o^2} \bar{\lambda}_2^2)\, v_2^2$$

$$+ (c_1 + cc_2)\, v_1 v_2 \Big]\, dxdy \qquad (8.21)$$

which gives the following condition for the function V to be a Liapunov function

$$b_1 b_2 - c_1 c_2 + \frac{b_1 \bar{\lambda}_2^2 \bar{u}_2}{\bar{V}_o^2} + \frac{b_2 \bar{\lambda}_1^2 \bar{u}_1}{\bar{U}_o^2} + \frac{\bar{\lambda}_1^2 \bar{\lambda}_2^2 \bar{u}_1 \bar{u}_2}{\bar{U}_o^2 \bar{V}_o^2} > 0 \qquad (8.22)$$

where $\bar{\lambda}_1$ and $\bar{\lambda}_2$ are the roots of the equation obtained after simplifying (A6) by using matching conditions (A4) and boundary condition (A5). Thus, the sufficient condition for nonlinear stability of the equilibrium state in the region A is given by (8.22). The equations for determining $\bar{\lambda}_i^2$; i=1,2 are given by (A11), (A12) in cases of habitats with two and three patches respectively. As discussed in Appendix, the minimum root of these equations increase with dispersion in patchy habitat, it can be concluded that the region of stability obtained from the condition (8.22) increases with increasing dispersion coefficients in patchy habitat.

In a particular case when crowding terms in interaction functions for the two species are zero, i.e. $b_1=b_2=0$, it can be noted from (8.11) and (8.14), that the equilibrium state which is unstable without dispersion may become linearly stable

provided

$$\bar{\lambda}_1^2 \ \bar{\lambda}_2^2 - c_1 c_2 > 0 \tag{8.23}$$

[see equation (8.16)]. However, from (8.22), the region of nonlinear stability can now be obtained from the following inequality

$$\bar{\bar{\lambda}}_1^2 \ \bar{\bar{\lambda}}_2^2 - c_1 c_2 > 0 \tag{8.24}$$

Comparing (8.23) and (8.24) with (8.16), (8.22) it can be remarked that the effects of crowding with dispersion in a patchy habitat are to increase the degree of linear stability and region of nonlinear stability.

Further it can be noted from (A9) that in the case of one dimensional habitat where $D_{ijy}=0$; $i=1,2$; $j=1,2,\ldots N$, the region of nonlinear stability is smaller than that in the two dimensional habitat. Thus the equilibrium state which is nonlinearly stable in a two dimensional habitat may not be so in a linear one dimensional habitat.

8.4 PREY-PREDATOR MODEL

In case of prey predator model, the Volterra type of interaction functions are given by

$$\begin{aligned} f_{1j}(u_{1j}-u_{2j}) &= (a_1-b_1u_{1j}-c_1u_{2j})\, u_{1j} \\ f_{2j}(u_{1j},u_{2j}) &= (a_2-b_2u_{2j}-c_2u_{1j})\, u_{2j} \end{aligned} \tag{8.25}$$

which gives the positive equilibrium state as

$$\frac{a_2c_1+ a_1b_2}{c_1c_2+ b_1b_2}, \quad \frac{a_1c_2- a_2b_1}{c_1c_2+ b_1b_2}$$

provided $a_1c_2-a_2b_1 > 0$. The linearized system can be given by (8.3) with

$$\begin{aligned} b_{11} &= -b_1\bar{u}_1 \; ; b_{12} = -c_1\bar{u}_1 \\ b_{22} &= -b_2\bar{u}_2 \; ; b_{21} = c_2\bar{u}_2 \end{aligned} \tag{8.26}$$

To see the linear stability of the equilibrium state, the same positive definite function E as (8.12) is considered, from which, proceeding as before, it can be noted that E is a Liapunov function as the condition (8.14) in this case is automatically satisfied. Thus the equilibrium state which is linearly stable otherwise would remain so with dispersion in patchy habitat. The same result is true for nonlinear stability also and this can be verified by choosing same Liapunov function V as (8.17).

8.5 CONCLUSIONS

In this chapter, the effects of patchines arising out of variable dispersion coefficients on linear and nonlinear stability have been studied by using Liapunov second method.

In the case of competition model it has been shown that the otherwise stable equilibrium state remains linearly as well as nonlinearly stable with dispersion in patchy habitat. However, if the equilibrium state is unstable without dispersion

the necessary and sufficient conditions for the linear stability of the equilibrium state in the positive quadrant has been obtained. But in the case of nonlinear stability with dispersion it can be seen that the equilibrium state could only be stable in a subregion of positive quadrant and this region would increase with increasing dispersion.

In case of prey-predator model, the otherwise stable equilibrium state remains stable linearly and nonlinearly with dispersion.

APPENDIX

Let us consider

$$I = \sum_{j=1}^{N} D_{ijx} \int_{L_{j-1}}^{L_j} \left[\frac{\partial u_{ij}}{\partial x} + h_{ij}(x)\, v_{1j} \right]^2 dx \geq 0 \qquad \text{(A-1)}$$

where h_{ij}, $i=1,2$; $j=1,2,\ldots N$ are arbitrary differentiable functions in $L_{j-1} \leq x < L_j$.

The integral (A1) can be simplified to get

$$\sum_{j=1}^{N} D_{ijx} \int_{L_{j-1}}^{L_j} \left[\left(\frac{\partial v_{ij}}{\partial x}\right)^2 - (h_{ij} - h_{ij}^2)\, v_{ij}^2 \right] dx$$
$$+ \sum_{j=1}^{N} \left[D_{ijx}\, h_{ij}(L_j) v_{ij}^2(L_j) - h_{ij}(L_{j-1}) v_{ij}^2(L_{j-1}) \right] \geq 0 \qquad \text{(A-2)}$$

Let $h_{ij}(x)$ to be the solution of the following differential equation

$$h'_{ij}(x) - h_{ij}^2(x) = \lambda_{ij}^2 \qquad \text{(A-3)}$$

where h'_{ij} is the derivative of h_{ij} w.r.t. x and λ_{ij} being arbitrary real constant, subject to the conditions

$$D_{ijx} h_{ij}(L_j) = D_{i(j+1)x} h_{i(j+1)}(L_{j+1}) \; ; \; j=1,2,\ldots N-1 \qquad \text{(A-4)}$$

$$\underset{x \to 0}{Lt}\; v_{i1}^2(x) h_{i1}(x) = 0$$
$$\qquad \text{(A-5)}$$
$$\underset{x \to L_N}{Lt}\; v_{iN}^2(x) h_{iN}(x) = 0$$

Then $h_{ij}(x)$ can be determined as follows:

$$h_{i1} = - \lambda_{i1} \cot \lambda_{i1}$$
$$h_{ij} = - \lambda_{ij} \tan \{\lambda_{ij}x + A_{ij}\} \qquad (A6)$$
$$h_{iN} = - \lambda_{iN} \cot \{\lambda_{iN}(x-L)\}$$

Now substituting (A3)-(A5) in (A2) we get the inequality.

$$\sum_{j=1}^{N} D_{ijx} \int_{L_{j-1}}^{L_j} \left(\frac{\partial v_{ij}}{\partial x}\right)^2 dx \geq \sum_{j=1}^{N} D_{ijx} \lambda_{ij}^2 \int_{L_{j-1}}^{L_j} v_{ij}^2 \, dx \; ;$$
$$i=1,2 \; ; \; j=1,2,\ldots N \qquad (A\text{-}7)$$

Thus using (A-7),

$$\int_0^B \sum_{j=1}^{N} D_{ijx} \int_{L_{j-1}}^{L_j} \left(\frac{\partial v_{ij}}{\partial x}\right)^2 dxdy + \int_0^B \sum_{j=1}^{N} D_{ijy} \int_{L_{j-1}}^{L_j} \left(\frac{\partial^2 v_{ij}}{\partial y^2}\right) dxdy$$
$$\geq \int_0^B \sum_{j=1}^{N} \left[\left(D_{ijx} \lambda_{ij}^2 + \frac{D_{ijy}\pi^2}{B^2}\right) \int_{L_{j-1}}^{L_j} v_{ij}^2 \, dx \right] dy \qquad (A\text{-}8)$$

Assuming

$$D_{ijx}\lambda_{ij}^2 + \frac{D_{ij}\pi^2}{B^2} = \bar{\lambda}_i^2 \qquad i=1,2; \; j=1,2,\ldots N \qquad (A\text{-}9)$$

we get from (A8)

$$\int_0^B \sum_{j=1}^{N} \int_{L_{j-1}}^{L_j} \left[D_{ijx}\left(\frac{\partial v_{ij}}{\partial x}\right)^2 + D_{ijy}\left(\frac{\partial v_{ij}}{\partial y}\right)^2 \right] \geq \bar{\lambda}_i^2 \int_0^B \int_0^L v_i^2 \, dxdy \qquad (A\text{-}10)$$

where $\bar{\lambda}_i$ can be determined from (A6) and (A9) using the conditions (A4). In the particular cases of habitats with two and three patches, the form of equations determining $\bar{\lambda}_i$; $i=1,2$ can be written as

$$\cot\left(\frac{\bar{\lambda}_i L_1}{\sqrt{D_{i1x}}}\right) + \sqrt{\frac{D_{i2x}}{D_{i1x}}}\,\cot\left[\frac{\bar{\lambda}_i (L-L_1)}{\sqrt{D_{i2x}}}\right] = 0 \qquad (A\text{-}11)$$

and

$$\sqrt{\frac{D_{i2x}}{D_{i3x}}} + \cot\left[\frac{\bar{\lambda}_i (L-L_2)}{\sqrt{D_{i3x}}}\right].$$

$$\frac{\sqrt{D_{i1x}}\,\cos\left[\frac{\bar{\lambda}_i L_1}{\sqrt{D_{i1x}}}\right]\sin\left[\frac{\bar{\lambda}_i (L_2-L_1)}{\sqrt{D_{i2x}}}\right] + \sqrt{D_{i2x}}\,\cos\left[\frac{\bar{\lambda}_i (L_2-L_1)}{\sqrt{D_{i2x}}}\right]\sin\left[\frac{\bar{\lambda}_i L_1}{\sqrt{D_{i1x}}}\right.}{\sqrt{D_{i1x}}\,\cos\left[\frac{\bar{\lambda}_i L_1}{\sqrt{D_{i1x}}}\right]\cos\left[\frac{\bar{\lambda}_i (L_2-L_1)}{\sqrt{D_{i2x}}}\right] - \sqrt{D_{i2x}}\,\sin\left[\frac{\bar{\lambda}_i L_1}{\sqrt{D_{i1x}}}\right]\sin\left[\frac{\bar{\lambda}_i (L_2-L_1)}{\sqrt{D_{i2x}}}\right.}$$

$$= 0 \qquad (A\text{-}12)$$

respectively for equal dispersion coefficients in y-directions. The above two equations have been solved numerically in Chapter IV and it has been pointed out that minimum roots of these two equations increase with increasing dispersion coefficients in different patches.